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EDWARD ROYAL WARREN

1860–1942

BY T. D. A. COCKERELL

Nearly forty years ago, I called on Mr. Warren at Colorado Springs, and he showed me his collection of mammals, which he brought into the room on a tray. Not many years later he had to put up a small new building to contain his collection.

In spite of the opportunities for observations and discoveries, the amateur naturalists of Colorado have been few. In still earlier times, when the Californians undertook to do some zoological and botanical work on their own account, the movement was held up to ridicule by Bret Harte, and there were serious misgivings in other quarters regarding the capacity of the westerners to "paddle their own canoe." Perhaps these obstacles and inhibitions prevented the development of Rocky Mountain Zoology, and there seemed to be no special reason why Edward Royal Warren, a retired mining engineer, should graduate into the chief authority on Colorado mammals and a prominent student of Colorado birds. He himself gives the major part of the credit to William Lutley Sclater, son of the famous secretary of the Zoological Society of London.

I remember Sclater as a young man, when he returned from an expedition to South America, and appeared at a meeting of the Zoological Society, reporting on some new animals he had preserved. In course of time he went to South Africa to the Museum at Cape Town, and came to be closely identified with African Zoology. But he married a daughter of General Palmer, of Glen Eyrie, Colorado Springs, and was induced to move to Colorado, where he built a house in African style. In his new surroundings, he at once became acquainted with Warren and with the well-known ornithologist Aiken. Warren tells how Sclater planned to write a book on the Mammals of Colorado, but found it required more time than he could spare. He accordingly turned to Warren, proposing that he should do it. Warren had been actively interested in the mammals of Colorado since 1902, and was well prepared to carry on this work, though he probably would not have undertaken to do it but for Sclater's encouragement. The whole story illustrates, first of all, how men capable of doing important scientific work may be found here and there in the population; and secondly, how they may be brought to fruition by the right kind of encouragement at the right time.

Of all the animals studied by Warren, he was most attracted by the beaver. This led him to make a detailed study of the beaver's habits, which formed the basis of the second Monograph published by the American Society of Mammalogists (1927). This was followed by The Beaver in Yellowstone National Park, and the Beaver in Estes Park, published in the Annals of the Roosevelt Wild Life Experiment Station, with which Warren was associated from 1921 to 1928. It was assumed that the Colorado form was referable to *Castor canadensis frondator* (Mearns), described from Sonora. In "Zoology of Colorado" (1927), page 48, I pointed out that there was at least some difference, and careful studies made later by Warren and E. R. Hall showed that the Colorado animal should be separated as a subspecies, which (Jour. Mamm. 1939, p. 358) was named *Castor canadensis concisor*.

The marmots were all referred to a single form, *Marmota flaviventer* in the Mammals of Colorado. But Howell, with more abundant materials, showed that the true *M. flaviventer* occurred in Oregon and California, and separated out several races in Colorado. One of these, found from Garfield County to Saguache County, he named *M.f. warreni*. Still more recently (Jour. Mamm., 1934, p. 62) Warren described the marmot of the Wet Mountains of southern Colorado as *M.f. notioros*. Two other Colorado mammals have been named after Warren. The cottontail of southwestern Colorado, ranging into Utah, New Mexico, and Arizona, is *Sylvilagus auduboni warreni* Nelson. A wood-rat, known from Baca and Las Animas counties, is *Neotoma albigula warreni* Merriam. A gall insect on oak, discovered by Warren at Trinidad, Colorado, but also found in Arizona and Texas, is *Callimome warreni* (Cockerell). The Evening Grosbeak found in Colorado, one of our most characteristic birds, is *Hesperiphona vespertina warreni* Grinnell. A beautiful white-flowered species of azalea, found in the mountains of Colorado, is *Azaliastrum warreni* A. Nelson.

Warren was associated with the Colorado College as honorary Director of the Museum for a time, but took no part in the teaching. He was a member of various scientific societies, and a contributor to the Journal of Mammalogy, the Colorado College publications, the Proceedings of the Biological Society of Washington, The Condor, the Auk, etc. His account of the small mammals of Colorado, published by the Colorado Mountain Club in 1921, was widely used and appreciated.

By Robert W. L. Potts

Born at Waltham, Massachusetts, in 1860, Mr. Warren first came west out of Boston, a young man to a young man's world—the roaring Colorado mining camps of the early eighties. He was an assayer and engineer around the fabulous Gunnison region, the Taylor River, Crested Butte, and Gothic of the Wolverine Basin in the West Elks. In 1936, I went through much of the same region with him again, after Pittsburg and Gothic and many another town had gone through not only the ghost stage but had vanished altogether. He pointed out the beaver ponds where he had camped so that at the end of a day's traverse he could

observe and record all he could of that industrious animal. We collected a marmot on the same boulder, shooting from the side of our car, which stood where his wagon had back in '82, where he collected his first.

Almost fifty years had gone by. It should be a nostalgic picture, but it held none of that. Mr. Warren was of that great breed of men whom the years may slow, but otherwise leave untouched. Unable to manage a camp alone, partially deafened, years past the time when most men take to the softest chair, Mr. Warren was at his best. Often he tramped for miles in that rough, mountain country to come in weighted with marmot, rabbit, coney, and weasel. When he couldn't be out on his long summer camping jaunts he was never quite proscribed by the walls of his stacked and littered study. It bulged with notebooks filled with the notes from his trips or reading; bulged with texts and separates; bulged with letters from the hundreds of correspondents, county clerks to scientists, who had answered or attempted to answer the numberless questions that had occurred to Mr. Warren's perpetually questing brain. Always, too, there were half a dozen different studies or papers that he worked on.

For all the dynamo that drove him, he was one of the quietest, and the most contented men I ever knew. Seldom applied to any man, and strange sounding in particular when applied to a real one, the adjective "sweet" sums up a great deal of Mr. Warren's character. His home, his wife, and his two daughters were an integral part of him, and his home was a rendezvous for all. Being partially deaf, it was often difficult to include him in the swift chit-chat of the frequent gatherings, yet he was by no means a specter at the edge of the feast. He sat aside, watching, smiling, perhaps not hearing as well as most, but everyone felt his presence. He was no less the host, and he missed little or none of the fun. Our dog, a snooty and independent little Sealyham, a one-family dog if ever there was one, adopted Mr. Warren at first blush, and we might as well have not been around when he was there. The Warrens' two cats slept in his lap by choice over the softest chairs, not that he petted them much, or froliced with them. They sensed his quiet kinship, just as did all who met and knew him.

He was so quiet and unobtrusive that probably only a few realized how dauntless was his nature. I often found myself wondering, when we were out on our long summer trips, whether he just never saw the dangers or difficulties, or whether he did and got a certain devilish satisfaction out of beating the game. We went skidding and bumping over many of the oldest and worst roads in New Mexico and Colorado on those trips after small mammals. One time we were heading northward over an old cart track out of New Mexico toward Pagosa Springs. We had been through rains and semi-floods all day, with chains on all four wheels. We were just easing our way across a rickety old bridge when we saw a bore of water some three feet high come swirling down the narrow gulch. Barely safe across we paused to watch it cover the bridge. "I thought for a moment," said Mr. Warren, "that we might have to get out and put a chain on the spare tire."

Another time we had a right rear tire blow out on our heavily laden car as we were sailing along the fine road to Salida, for Mr. Warren liked me to drive fairly

fast when the roads were good. When I got out of the car my knees were quaking. Mr. Warren got out of his side and looked over to a nearby tree; the midday heat of that high plain was immediately noticeable. "Well," he spoke softly, "if you'd only skidded it a few feet further we'd have been in the shade."

And once we tried to drive a car up the side of lofty Mount Sierra Blanca. Following old mine survey maps, our modern one still showed an "unsurfaced road, safe in dry weather" some third or more of the way up its bleak side. After trying to trace it after it had "petered out" in a rocky chasm, I wanted to back up to a flat spot, and turn around and go elsewhere. Not Mr. Warren. "The map shows a road," he persisted, as though maps were irrefutable, but really because it was his sole remaining argument.

"Nope, no road," said I. We had already driven better than a mile beyond the last remnants of decency.

"Try that last gulch we saw," Mr. Warren directed equably, "Maybe that's where the road went."

"Let's turn around while we can." I had sounded the same plaint before and advanced the suggestion without hope.

"The map . . ."

"I know," I broke in, putting the car in low and starting out once more, "the map shows a road." On we drove, on and up, pounding the big old Buick over rocks, brushing aside the limbs of the tough and wiry Piñon pines, jacking a wheel over a rock here, piling Piñon bows into a hole there. Finally even Mr. Warren would admit the utter non-existence of a further place to put a tire. But only a sheer wall and the lateness of the hour stopped our trying. We'd driven two thousand feet up the side of that steep cone beyond the feeble road that had led us up out of the flat Alamosa Valley, far beyond where auto ever went before. I was at the wheel but Mr. Warren's was the enthusiasm that kept the old car going.

He was as dauntless about such a thing as he was about life itself. When he broke his leg just before the meeting of the American Society of Mammalogists in Denver in 1940, there was but one foregone conclusion . . . if he lived (and for as old a man as he, that "if" loomed tremendously large) he would never walk again. Bedridden, his leg under terrific traction, steel splinted and plastered, he grew worse; uremic poisoning developed, became severe. Mr. Warren's smile was as sweet as ever, withal so terribly weak. He fumbled for a letter he had just received from several members of the Society, men with whom he had worked over his beloved mammals. I must read it; they missed him and some were even coming down to see him. "I guess maybe I won't get to the meetings this year," he whispered, "but I'll be extra careful just before the next one."

And that indomitable courage pulled him through . . . and he walked, first with a heavy brace and crutches, in a few months without even those aids. The first time I saw the miracle, he came pulling a little wagon out of the backyard with wood for his fireplace in it. "I guess you just can't kill a Warren," murmured the doctor who had attended him.

In many years of knowing Mr. Warren, I never knew him to express anything

derogatory to another's character, with only a single exception. He saw everything with the truly tolerant eye, and to him every man was a friend. His was completely the kindly, common touch. Often we were plagued on our trips by curious sheep herders, reminiscing cowboys, or the hardier-than-most tourist who had somehow managed to get into the same high country where we always camped. Mr. Warren didn't know how to turn them away.

His exception to the rule? Oh, yes. One year I was unable to go out with him. We found a young fellow to take my place. Mr. Warren came home, enthusiastic. It had been wonderful to have someone in camp who was always chasing off to look at the other side of a mountain when he wasn't out mammal collecting. Mr. Warren had never been able to understand how I was content to lie for hours in the shade of a tall spruce tree on a long mountain slope. But he twinkled at me, for all his sly digs.

His interests were alert, keenly so. To all the struggling young fry just beginning, he gave a willing ear and over-generously of his time and assistance. And always his mind was young and open. He loved new ideas, and was eager to know the new approaches in all fields. Above all, perhaps, he had balance, seasoned with warm kindliness. Too, he had strength, and his last years were lived in a white heat of mental intensity, driving a body that completely refused to be licked by the years. His sister, who was so like him in many ways that they might have been twins, once complained, "I used to know so many nice old people . . . it's funny, there just don't seem to be any old people around nowadays."

He achieved much, quietly, which is an achievement in iteslf. He was widely admired without stint. All who were fortunate enough to know him recognized that here was a man who had fully lived his life, and that he had found his peace. Men like that never die; they live as stars on our horizon.

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WOOD RATS (*NEOTOMA ALBIGULA*): THEIR GROWTH AND DEVELOPMENT

By William B. Richardson

The study of the wood rat with special emphasis on the growth and development of the young from the time of birth to subadulthood, was undertaken between February and August of 1940. This work was a part of the Archbold Expeditions' program carried out at a temporary biological station situated at the foot of the Rincon Mountains, 20 miles east of Tucson, Arizona. I wish to express my appreciation to the leader of our group, Mr. Richard Archbold, who made this work possible.

Throughout the Tucson region, wood rats were common as evidenced by their nests. In the valley they nested usually in prickly pear clumps or about the bases of creosote bushes, where they often utilized abandoned ground squirrels' (*Citellus tereticaudus*) burrows. In the foot-hill region, rocky outcrops with their cracks and crevices afforded the usual nest site. For detailed information on habitat and abundance of these animals in this region see Vorhies and Taylor (1940, pp. 461–513).

My stay was within the limits of the breeding season, which, according to Vorhies and Taylor (1940, p. 473), extends from January through August. The animals for study were obtained in live traps or dug from the nest and housed in large cages. Mothers with their young were under daily observation and notes and records were compiled. Although the bulk of the information came from observing these caged animals, wherever possible it was supplemented by field notes.

GESTATION PERIOD

Frequent attempts to induce captive animals to breed failed. However, a number of pregnant females, which at the same time were suckling their young, were captured and caged apart from mature males. For example, a female taken March 15 had two young whose eyes opened on March 17. This same female gave birth April 21 to two young whose eyes opened on May 5 after a period of 15 days. Assuming that the eyes of the young of the previous litter likewise took 15 days to open, we may place then the date of birth of the previous litter as March 3. From this we may conclude that the gestation period is at least 37, perhaps more than 38, days, that insemination may occur in the first 12 days after the female gives birth to young, and that in this case there was a 49 day period between litters. The usual size of a litter is two with three as the maximum. The gestation period of this species appears to be considerably longer than that of *Neotoma fuscipes annectens*, which, as recorded by Donat (1933, p. 24), "probably . . . is 23 days" or that of *Neotoma micropus*, which, as reported by Feldman, (1935, p. 301) is less than 33 days. The potential increase in progeny is considerably slower and lower than that of *Rattus norvegicus*, which has a gestation period of 21 to 26 days, a litter average of 7 to 8, with sometimes as many as 20 young, and a possibility of a 28 day period between litters (Lantz,

PLATE 1

Adult female transporting young, one held in mouth and other attached to nipple.

PLATE 2

Adult female disturbed from nest. Note young of about 45 days clinging to nipples.

1909, pp. 15–16). My findings concerning the gestation period disagree, however, with those of Feldman (1935, p. 301) who states that "Gestation in . . . *N. albigula* is less than 30 days . . . based on . . . the minimum time between successive litters."

NEW-BORN YOUNG

The new-born young (see Plate 1) are nearly twice as large as those of *Rattus norvegicus*. They weigh on the average 10.9 grams, as compared with the 5.2 grams of *R. norvegicus* (King, 1923, p. 81). The ventral coloration of *Neotoma*, including legs, ears, and muzzle, is pink; dorsally it shades into a gray produced by hair follicles and the short, dark-based hair (1 mm in length). The skin appears poorly fitted to the body, having large rolling folds over the shoulders, about the flank, and at the base of the tail. In addition there is a scaly appearance to the skin as if the epidermis were sloughing. The eyes are tightly closed and only the bulge and the obscure slit of the unopened eyelids mark the place they are to appear. The ears are closed, the pinnae being folded downward and sealed to the sides of the head, completely concealing the auditory openings. The legs are short and weak, being unable to support the body weight. The feet in proportion to the body are large with short, distended claws on chubby, spreading toes. The head is oval in shape without the pointed muzzle as found in the adult. The vibrissae, measuring up to 12.0 mm in length, protrude from an inflated upper lip. The tail is short, fleshy, and hairless. The incisors, both upper and lower, are present, but short, separated, and with incurved hooked tips to facilitate grasping the nipple. Averages, maxima and minima of weights and measurements of 9 to 12 new-born young are as follows:

	Average	Maximum Minimun
Head	24.1 mm.	(25.4 – 22.7)
Head and body	59.7	(62.7 – 56.1)
Tail	26.1	(28.1 – 23.0)
Hindfoot	12.7	(13.3 – 12.3)
Ear	5.7	(6.6 – 5.3)
Weight	10.9 grams	(12.5 – 9.3)

PERIODS OF DEVELOPMENT

Growth and development of the wood rats is a more or less gradual change from birth to maturity. There are, however, during this change certain periods when development is more apparent, when rather sudden changes appear in the life of the young accompanied with different reactions to the environment. These breaks are here used to separate the development into periods, thus simplifying explanation. The first period is from birth until the eyes are opened. The second includes the time from the opening of the eyes until the young are weaned. The third includes from weaning to maturity (adulthood).

FIRST PERIOD OF DEVELOPMENT

The duration of this period is from birth to the opening of the eyes on the 15th to 19th day. During this time the principal change is in physical growth. There

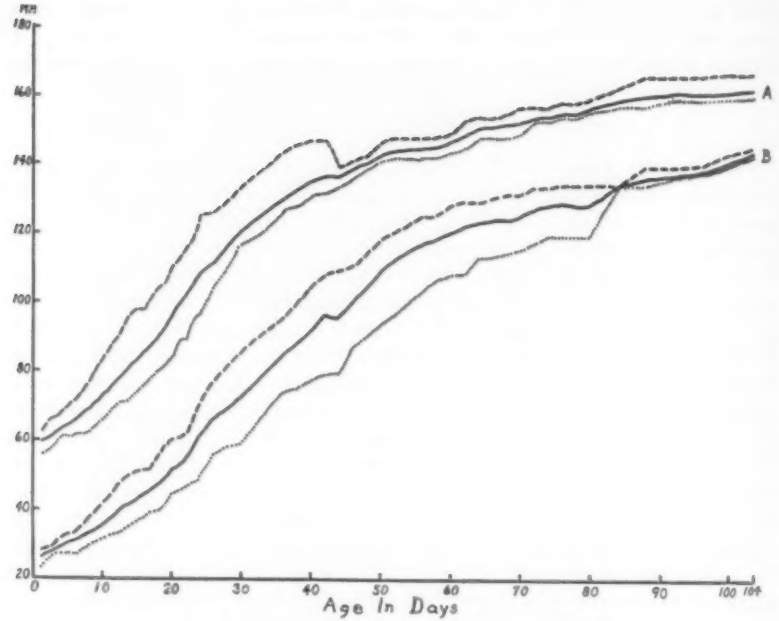

FIG. 1. Growth rate of (A) head and body, and (B) tail, of *Neotoma albigula* from birth to 104 days of age with solid line representing the average, broken line the maximum, and dotted line the minimum. The number of animals on which the graph is based is as follows: 11 to 9 for the first 42 days, reduced to 4 by the 50th day, and to 3 on the 84th day.

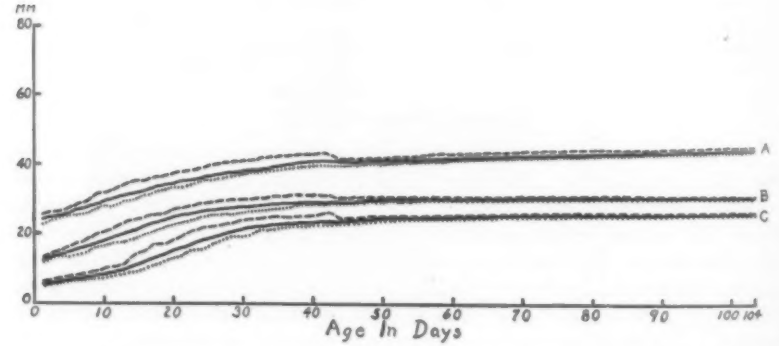

FIG. 2. Growth rate of (A) head, (B) hind foot, and (C) ear of *Neotoma albigula* with the average represented by a solid line, maximum by a broken line and minimum by a dotted line. The number of animals on which the graph is based is as in fig. 1.

is rather rapid increase in size with a lengthening of the rostrum. The foot assumes a normal shape with divided toes and well defined tubercles. The pinna rises during the first day or two and increases in size, with the auditory canal opening on the 13th to 15th day. The fuzzy coat changes to that of the sub-adult pelt, which covers the body in a pattern similar to that of the adult. The incisors lose their recurved hook and the molariform teeth appear. The vibrissae become longer and stronger, protruding from a less bulging upper lip.

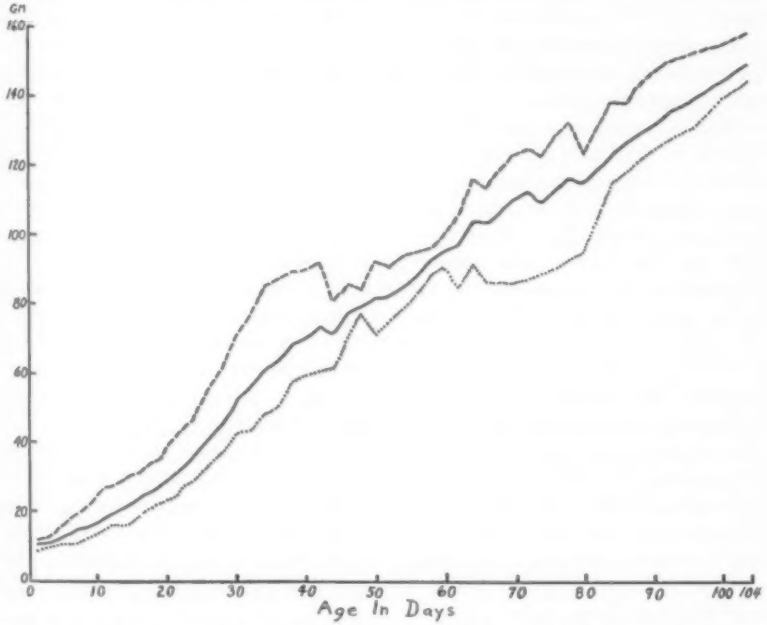

FIG. 3. Weight of a growing wood rat *Neotoma albigula* with the solid line representing the average, the broken line the maximum and the dotted line the minimum. The number of animals on which the graph is based is as in fig. 1.

The activity during this period is rather limited, for the young spend most of their time attached to the nipple except when they dislodge themselves to search for one of the other three nipples or on occasions when they are forcibly removed by the mother. Suckling is often accompanied by a quivering or kicking movement which may be exercise necessary in strengthening the young. During this period the young learn the fundamentals of walking, although they do not become very steady on their feet. They are able to right themselves awkwardly when turned over. Unattached on an inclined plane, they struggle to brace themselves against slipping. When dropped from a height up to 18 inches they make no apparent effort to right themselves on the way down. During the latter part

of this period, the young have been observed scratching about their ears and vibrissae with the hindfoot, followed by licking the toes of the foot used in scratching. They also clean their muzzle with their front feet. This grooming is not uncommonly indulged in so vigorously that they upset themselves, but regardless of the fall, they continue the grooming for several seconds.

When attached to the nipple, the young remain relaxed with little regard for their position. Thus attached, the female transports the relaxed young wherever necessary, the young dragging along without regard for equilibrium. When the female is excited, I have seen her run about the partially destroyed nest with the young dangling behind, bobbing over the debris. Not infrequently, however, the female will remove one of the young which is attached to the nipple by grasping the young one's belly with her incisors and giving a twist and a pull. This method of removing young differs from that used by *Neotoma fuscipes macrotis* as recorded by Gander (1929, p. 57): "A captive female with three young was observed to disengage herself from the young by turning around and around until two of them has [sic] become detached, and the forepaws were used in freeing herself from the third." The female holding the quiescent, coiled young by the belly (see Plate 1) may thus transport it from place to place with ease.

Removing the young from the mammae to weigh and measure them, was at first quite a problem. Pulling on the young stimulated a firmer grasp and excited the mother, with the result that when finally removed they usually tore the skin of the nipple. However, I found that by taking the young between thumb and forefinger and turning it around several times, it would release itself without injury and without excitement to the female or itself.

It was also found that young of this period would suckle and attach themselves to a cut end of a rubber band. Once affixed to the rubber, the young relaxed and in this condition they could be pulled about my desk, over books, and other equipment, all the while remaining in the reposed position. The young would hang dangling at the end of the rubber for an indefinite period of time. Thus hanging, young of 15 days could easily support a weight of 150 grams attached to its hind legs.

The senses in the young, with the exception of touch, are poorly developed or entirely undeveloped. The eyes are closed. The ears are sealed except for the last two or three days when sound recording is probably imperfect. Concerning taste and smell, I have no information. Touch, however, is developed and serves importantly in the well-being of the young. Touching the vibrissae or hair stimulates a positive response; that is, movement toward the object stimulating. Accompanying this movement is a turning of the body on its side or back and a pawing with the front and hind feet. This response is a typical reaction of the young to the mother in the attempt to reach the mammae. When the nipple is once gained the young do not further react to the stimulus of touch. Moreover, this response to the female can easily be reproduced by placing a piece of cotton near the young. When the cotton is touched, the young immediately move toward it, turning themselves on their sides or backs and pawing the cotton fibers. This specialized reaction under ordinary circumstances is valuable to the young in finding the mother's nipples. However, the young have been seen giv-

ing this same response to members of an older litter, to others of their own age, as well as to nest materials. One wonders if this reaction, seemingly important in early life, does not at times lead the young into difficulty.

Usually the female appears to give little aid to the young in finding the nipple. On several occasions, though, I have seen the female reach out, pick up a young in her mouth, bring it back to the nest, and release it between her front legs; whereupon it immediately crawled toward the teats, turned and attached itself. To facilitate its last efforts the female raised her body until the young had gained the nipple.

The mother takes care not to step on the young, but occasionally she does so, which brings forth a squeak from the young and the subsequent moving of her foot. When the rats are very young this squeak is usually muffled, sometimes so muffled as not to be audible to the human ear. As the animal becomes older the voice is louder but less often used, the use being limited mainly to times of distress as when detached from the female or when the young are injured.

The urine and feces are passed only on stimulation of the genital region. This is accomplished by the female licking the genitalia and occasionally pressing with her front feet on the abdominal region of the young. The young relax and emit, whereupon the urine and feces are consumed by the female. This function is frequently accompanied with squeaks from the young as if in pain.

SECOND PERIOD OF DEVELOPMENT

The second period is one of play, where the activities develop into patterns later used in independent life. It begins about the 17th day, when the eyes open, and lasts until weaned which may be from 45 to 55 days (62 to 72 days from birth), depending in part upon the time the following litter appears, and probably upon the food supply, the temperament of the female, etc. These young wood rats are able to take care of themselves under ordinary circumstances 25 to 30 days after their eyes open or about the time the following litter appears. The young, although able to care for themselves, remain about the nest receiving less attention from the female, but continuing to suckle beside the younger offspring when possible.

The color and pattern of the fur of the young are essentially like that of the adult, differing slightly in being grayer and less dense but completely covering the body. The recently opened eyes measure 6.5 mm from notch to notch. The ears are open, the pinnae up, furred, and movable; that is, they may be twitched or laid back along the head. The head is lengthened with a more pronounced muzzle, the general contour approaching that of the adult. The vibrissae vary in length to 30 mm, arising from an apparently less bulging lip than that of the younger animals. They are dark brown or black with silver tips, the silver color being dominant on dorsal and posterior vibrissae. The legs and feet are larger, more muscular, and capable of supporting the body, even while the rat clings to the sides or roof of the wire mesh cage. The tail is lengthened, haired, and less chubby in appearance. The incisors are only slightly incurved, the hook apparent at birth having disappeared. The voice is still the squeak of infancy.

It is during this period that the physical growth is most rapid (see figs. 1 and 2).

The hind feet and ears reach their full size, whereas the head, body, and tail continue to grow, having their most rapid increase at this time. The weight, unlike the body measurements, has a relatively regular increase. The curve as plotted on the graph (fig. 3) shows no signs of tapering off in the later part of this period. The weights and measurements of the beginning (17th day) and end (66th day) of this period are as follows:

	17TH DAY (10 INDIVIDUALS)		66TH DAY (4 INDIVIDUALS)	
	Average	Maximum Minimum	Average	Maximum Minimum
Head	33.5 mm.	(36.0–31.9)	42.7 mm.	(43.5– 42.4)
Head and body	88.0	(101.5–78.5)	151.0	(154.0–148.0)
Tail	45.5	(52.0–39.3)	124.0	(130.0–113.0)
Hindfoot	23.0	(25.9–20.2)	31.0	(31.2– 30.8)
Ear	13.5	(17.3–11.1)	25.8	(26.4– 25.2)
Weight	25.2 grams	(32.6–20.4)	103.3 grams	(113.9– 86.1)

There is a fear of falling as shown by the fact that the young wood rat will not crawl off the edge of the scales, as it did before the eyes were open. When dropped from a height of 6 inches it has the ability to right itself. Thumping of the ground with the hindfeet had appeared in young of 26 days of age. They are less active during the earlier part of the period, as much of their time is spent suckling.

Play is most apparent during this period. Throughout the earlier part, all free time consisting of short intervals between nursing, is spent in play. The young wood rats never lie idle, detached from the nipple. Later the nursing time decreases, play time increases, and not infrequently the unattached young will be found resting by the mother's side. Play as it occurs consists of frolicking about the cage, picking up objects, carrying, nibbling, digging, grooming, and exercising the body. When play is finished the young return to the mother's side to nurse or rest. This play appears as an activity without apparent immediate value to the player except as a release of surplus energy to develop the muscles and to acquaint the senses with objects or materials. As diversified in scope as is this play, it contains what we might call the pre-activities of the mature animal. These are apparently instinctive and remain as such until gradually they are put to use. Thus play may improve the acts, molding or refining them, to be useful at a later period.

The independence from the mother develops gradually with the most abrupt break occurring about the time the female gives birth to the following litter. With the arrival of the new young, the female does not aggressively attack or ward off the older litter; she permits them to suckle, although actually giving them less attention than before.

Mouth suckling of the female by the young was not infrequently observed during the latter part of this period; it was accomplished by the young turning their heads to one side and locking incisors with the female, and in this position the mouth was suckled from 15 seconds to several minutes at a time. This suckling

was indulged in more by some young than by others. Sometimes it began several days before the arrival of the following litter. The most logical explanation seems to be that at this time the mother's milk is insufficient for the rapidly growing young, and they, attracted by the moist mouth of the mother, begin suckling. Although not observed, liquids including the digestive juices and possibly even pre-digested food may, in this manner, be taken from the female's mouth. Thus, the young may be tided over until a time when they are more competent to care for themselves.

Learning to utilize solid food is perhaps one of the most important activities of this period. To find and distinguish food is manifested first as a part of the play pattern. The observed young have been seen picking up and nibbling on such things as bits of wood, grains of sand, cotton, the mother's tail, scats, as well as the various food stuffs in the cage. With the decrease in available mother's milk and an increase in food needed, it becomes necessary for the young to supplement the milk diet with such food as can be procured. As this need for food develops, trial and error supplements play with the tasty articles coming to attract more attention. Thus, gradually from play through trial and error, the young wood rats learn to differentiate food and how to feed themselves.

The incurved incisors, so apparent during the first part of the earlier period, now resemble the normal adult tooth. With this change and the increase in body weight, the young use another suckling posture (see Plate 2). When the female is quiet they assume an upright position—not the relaxed random posture of babyhood. When the female is in motion, rather than being dragged along, they follow behind her with a nipple held tightly between their incisors. If the youngs' pace is slower, the female will drive them off. This is due perhaps to excessive pressure applied to the nipple. Not infrequently the young will lose hold involuntarily with the sudden movements of the female, the teats being yanked out of their mouths before they have an opportunity to close on them. When the end of a cut rubber band is placed in the mouth of young about 40 days' old, they attach themselves and begin suckling in much the same manner as at an earlier period. They do not, however, relax. Rather they remain upright, bracing themselves against a forward motion but run after the band when sufficient pressure is applied. When held in the air attached to the rubber, the rat struggled continually, kicking its feet and swirling its tail in an effort to bring itself to a horizontal position. After struggling for about 30 seconds it released its hold, dropping to the ground. This experiment was repeated several times with the same result.

Cholla cactus, which was eaten by the wood rat, is a food requiring special handling. This cactus, with its profuse barbed spines, was commonly found throughout the area in which we worked. Yet regardless of its spines it was used by the wood rats as a source of food and water. The young during this period learn to manipulate and eat cholla as well as to extract its thorns from their flesh. The first contact at the earlier part of this period produces a negative response, a drawing away from the spiny object. This is shown by the two young (eyes open three days) that were observed playing over a small sandy

area on which several segments of this cactus, sticks, and rocks had been placed. One individual accidentally bumped into and stuck to a section of cactus. It uttered several squeaks and began a struggle which lasted two or three seconds before freeing itself. It then moved away from the vicinity of the cholla. The other young playing nearby also moved and the two continued their play for the ensuing hour away from that area. From this, their first lesson in spines, it appears that one individual learned from contact something of the nature of cholla and the second seemed to have learned from the experience of the other. As the need for food increased, the young were seen feeding upon the cortex of the cholla; it having been exposed by the female in her eating. While feeding on the open end of the segment, the young learn to nip away the areoles of spines thus exposing the juicy inner part. Later they acquire the ability to open the cholla for themselves by starting at the stem end of the segment where the spines are shorter and less numerous.

The passing of urine and feces during the early part of this period is stimulated by the female licking the genital region of the young. This method of voiding is, however, soon discontinued and the young are left to void for themselves. They do so with little regard for defecation areas, often rubbing their genital region on the floor of the cage to stimulate emission. This haphazard use of the cage for defecation soon changes. Within 10 days after the eyes open, the young, as do the adults, use one corner of the cage as the customary voiding spot.

Nest building and cleaning activities appear rather early in this interval as a part, or associate, of play. Nesting and cleaning first appear as random moving here and there of any small objects which may be found in the cage. Thus the young expend energy in doing acts which have no apparent immediate value, for such activities are carried out irrespective of the purpose of moving or the thing to be moved. For example, the young were observed transporting scats from the nest to the side of the cage and then turning around and moving them back into the nest. On other occasions they were seen carrying bits of nest material to other sections of the cage and laying them down as if starting a nest. After one to several trips, and sometimes an attempt to spread the insufficient material into a nest, the project was forgotten and the rat continued playing or returned to its mother. Later it might remove all or part of these bits of nest material to still another place in the cage or possibly return them to the original nest. With an increase in age of the young, however, there was a change from the haphazard toward the constructive. Young of 30 days were observed carrying bits of nest material (cotton) to a corner of the cage, making some 10 to 15 trips until a small area was covered, temporarily utilizing it for a nest. Such nests were never used for more than half an hour at a time before they were abandoned in favor of the home nest.

On one occasion a young of about 40 days was observed carrying a 4 day old offspring of the succeeding litter in the same manner as that used by the mother. Examination of the younger rat showed that no injury occurred during the brief time it was carried about the cage by the older inexperienced offspring.

Grooming was observed first in the previous period as an act of scratching the

ears and washing the face. This act, continuing throughout this period, was indulged in more vigorously and more frequently than during the preceding one. Combing the fur with the incisors like many of the other activities which appeared, emanated as part, or an associate, of play. For example, a young while scampering about the cage was observed to run upon its mother. It combed the fur about her back and ears in a vigorously playful manner for several seconds leaving the fur in a roughed state. Then it switched its attention to its own fur, combing it with better but still imperfect results. This combing of the pelt may be considered as play in that it served no immediate need, for at this time the female attended to that duty for both herself and her young.

There was a gradual improvement in agility with the developing of the wood rats' gaits, climbing, springing, balancing, and manipulating of their bodies. Locomotion changed from a spraddled awkward gait to one as agile as that of the adult. The young were seen frequently climbing over the sides of the cage and even walking across the top clinging to the wire mesh with the body suspended. During play, they often ran or chased each other about the cage springing to the side wall and off again, turning quickly, and stopping suddenly. Some were observed making an inside loop by springing up and backwards, glancing off the top of the cage and down to the floor again. This type of action was commonly found among caged squirrels and chipmunks, but only occasionally did it occur among wood rats kept under the same conditions. At the age of 45 days a young rat, when dropped two inches, was able to right itself and land on all four feet. Agility had apparently developed gradually through trial and error until adult proficiency was attained.

Digging and rolling in the sandy floor of the cage was observed during this time. Digging, the throwing of dirt to the side and backward with the front feet, was usually stimulated by the presence of fresh dirt in the cage; it was often accompanied by rolling in the loose dirt. Such activity might be considered an attempt to dust bathe.

The voice, the repeated metallic squeak so commonly used by the young during the first period, was heard less and less as this interval progressed until near the end it was completely unused. Early in this time, however, it might be heard occasionally as the young attempted to gain the teat or when injured, or occasionally as the mother groomed or stimulated defecation of the suckling young.

Up to the time the young of the following litter were born, the female made an effort to protect the previous litter by covering or carrying them away. With the birth of the succeeding litter, however, she paid less attention to the older offspring. This, coupled with the fact that they were heavier and their incisors were less adapted for holding the nipple, made it necessary for them to shift for themselves when in danger. Disturbed caged young were frequently seen running about the cage and hiding under the nest material or ducking behind the female. If cornered they attempted to ward off the intruding object with their front feet and, if grasped, they would attempt to bite. This fending was first observed in a young 19 days old (eyes open three days). The rat was to be removed from the cage and on reaching for it, it was seen to turn its forequarters to

the left side, raise its corresponding front foot, turn the head upwards, and expose its front teeth. Although it assumed this defense posture it made no effort to bite as it was taken up.

Fear as produced by a snake appears during this period.

THIRD PERIOD OF DEVELOPMENT

This period began about the 9th or 10th week (time of weaning) and continued until the animal had reached maturity. This was a period of maturing, the final development with the completion of growth and the perfecting of the various functions and activities into the adult pattern.

The duration of this period was in this instance unknown. Although several wood rats were followed from birth up to an age of 104 days, they were at that time still within this period. They were adult in some respects such as length of ear, length of hindfoot, length of vibrissae, as well as in many of the activities such as climbing, jumping, running, but sub-adult in such respects as length of head and body, length of head, and sexual activities. Feldman (1935, p. 303) states, "Maturity in body size and sexual development occurred in both forms [*N. albigula*, *N. micropus*] at about the age of 300 days. At this age their first breeding season was at hand."

Information gained on the wood rats during this period indicated the final development was a more or less gradual process becoming progressively slower until the adult peak was reached. The plateau of maturity was not reached suddenly, for some parts of the body as the hindfoot and others previously mentioned attained their adult size before others. Breaks in this development probably appeared with the maturing of sexual activities and as the animal was forced away from, or voluntarily left, his birth place in search of a new home. Perhaps the most pronounced change was in the development of the sexual structure and activity. I have, however, little information on this phase of the development except that it was during this period that the testes enlarged, protruding back of the anus and filling the scrotum.

The molariform teeth as shown by two individuals, one of 48 days, the other of 104 days, showed signs of wear; that is, a polish on the enamel ridges.

SUMMARY

A study was made of the wood rat *Neotoma albigula* with emphasis on growth and development.

In captive wood rats the gestation period is more than 38 days; insemination occurs in the first 12 days after birth of young, and two is the average litter.

The new-born young are large and pink, shading dorsally to gray. The eyes are closed, the pinnae sealed to the sides of the oval shaped head, the legs and feet weak, the tail short and fleshy. Four incisors have incurved tips.

During the first 17 days, or until the eyes open, the body size increases, feet assume normal shape, pinnae rise, auditory canals open, and the pelt becomes subadult-like. The young spend most of the time attached to their mother's nipples. When the female flees, the attached young bob along behind. The

female may take the abdomen of a young between her incisors and by giving a twisting pull remove the young to carry it in her mouth. The young walk awkwardly, right themselves when turned over, and scratch their ears and vibrissae with their hindfeet. A piece of cotton on their backs, stimulates the young to turn to their sides and commence pawing the fibers, a reaction typical when searching for the mother's mammae after contact with her body. Urine and feces are passed when the mother stimulates the genital area by licking it.

When weaned, 62 to 72 days, the young in color pattern are adult-like, the pelt slightly grayer and less dense. The body approaches adult proportions; the external ears open, the pinnae erect, moveable, furred; the tail lengthened and haired; and the incisors normal. Activity, increasing with growth, appears commonly in scampering about the cage, digging, preening, examining, nibbling, and carrying objects. Nursing, though continued, lessens after the following litter arrives. The young gradually learn to select and utilize solid food, even such items as the cholla cactus. Mouth suckling, although not common, is indulged in by some young. The young are soon left to void for themselves. Nest building and cleaning appear early and seemingly are associated with play. The metallic squeak soon discontinues. The young become too large to be cared by the female or to be dragged from danger by clinging to her nipples, thus they fend for themselves.

Weaning to maturity (over 104 days) completes the maturing of body form and processes. Adulthood is reached gradually with some activities and body portions such as length of hindfoot, length of ear, length of vibrissae, climbing, jumping, and running, attaining maturity before others.

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MAMMALOGY IN AN EPIDEMIOLOGICAL STUDY OF JUNGLE YELLOW FEVER IN BRAZIL

By Raymond M. Gilmore

Prior to 1932 yellow fever had been considered as strictly an urban disease, carried by the domestic mosquito, *Aedes aegypti*, in the classic cycle of man-mosquito-man. In 1932, however, the Brazilian Yellow Fever Service, an organization maintained by the Brazilian Ministry of Education and Health with the cooperation of the International Health Division of The Rockefeller Foundation, discovered the disease in a rural area in the *absence* of *Aedes aegypti* (Soper, *et al.*, 1933). This site, now historic from the standpoint of yellow fever, was the Valle de Chanaan, in the State of Espirito Santo, on the east coast of Brazil just north of Rio de Janeiro. The discovery marked a departure from the then current epidemiological beliefs regarding the disease, by calling for serious consideration of a different insect vector and a different vertebrate host (a jungle inhabitant) and also raised the question of possible control once the wild species in the newly discovered cycle were found.

In late 1935, I joined the staff of the Yellow Fever Service and participated in the field investigations, involving clinical, laboratory, entomological, and vertebrate zoological aspects, which were begun as a joint operation at a field laboratory at Anapolis in the State of Goyaz. Studies were continued there throughout 1936 and 1937; another field laboratory was set up in the southern Matto Grosso in 1937; and in 1938 Fordlandia on the Rio Tapajoz near the Amazon, and the vicinity of Rio de Janeiro were the scenes of continued intensive field work.

The solution of the problem of explaining all the epidemiology of jungle yellow fever is difficult, and is not yet complete; but it seems probable now (1941) that the disease is perpetuated by a cycle involving several species of wild mosquitoes and various mammals, especially monkeys and opossums. Control of these forms is not feasible, and an easily administered and effective vaccine has been developed as a solution to the problem of public health protection.

The demand on the zoologist in the beginning was for the collection of specimens of blood serum for an immunity (mouse-protection) test from as many vertebrates as possible, particularly primates. For it had been shown by laboratory and field investigations, on monkeys and man, that recovery from yellow fever infection conferred a specific and lasting immunity in these species. Therefore, it was concluded that any species of wild animal whose blood sera showed a high percentage of immunes, could be seriously suspected of complicity in the natural jungle cycle of the disease. This was an indirect method to be sure, but the only direct way to pin guilt on a species of vertebrate would be to isolate the virus from the circulating blood of a wild-taken individual. This would not be as easy, however, as it sounds, because (1) no susceptible animals are known to harbor the virus more than a week or so (generally 3–4 days) after infection—that is, there is no persistent infection, and (2) it would be necessary to guess several weeks ahead where yellow fever would occur in the human population

and get critical animal bloods there, because it was shown that susceptible wild animals around active human yellow fever cases generally were at the same time already immune and without circulating virus in the blood.

Some few vertebrates possess a non-specific immunity due to natural viricidal elements in the blood. These animals recently have been shown to include cattle and sheep, but not primates and marsupials, which have been demonstrated by extensive laboratory experiments to acquire immunity only after infection with yellow fever virus. The nature of the natural viricidal element is as yet obscure.

It was early decided that the best procedure to get the many blood samples desired for immunity tests was to catch the animals alive, and transport them to a field laboratory nearby for sterile bleeding, generally from the heart. The serum samples were later submitted to a central laboratory for an immunity test. (A mixture of a mammal serum and living yellow fever virus is inoculated in each of 6 white mice after a brain trauma with sterile starch to cause encephalitis. Recovery indicates immune bodies in the serum, and vice versa.) Thus, the immediate problem was to work out a technique to catch routinely as many vertebrates alive as possible, and to get an adequate quantity of blood serum. (An adequate blood serum sample, for the intraperitoneal protection test in white mice, was 3 cc, or 6 cc to provide for a retest if desired.) Such a relatively large amount of blood serum *demanded* that the smaller mammals and birds be caught alive and bled under ether; larger vertebrates could be shot and bled on the spot. Often several bleedings on a single small individual were necessary; and the serum from each was pooled. Later, however, when a "micro" (intracerebral) protection test was developed, which required but 0.5 cc of serum, and which was much more sensitive, it became possible to test adequately the smallest of mammals. Research on small birds benefited even more by this new technique.

To obtain the necessary amount of blood serum, special equipment, technique, and organization were required. The equipment consisted of live animal traps and accessories, transportation cages, bleeding and sterilizing apparatus, field bleeding outfit for victims shot, and paraphernalia for preserving specimens of all kinds in all ways. The organization consisted of a group of men to run trap lines; transport animals, men, and bait; care for animals; and aid with bleeding and sterilizing and with the preserving of specimens of vertebrates. The training of the necessary four to six men was so arranged that the absence of any one did not cripple the work.

So much by way of explanation. Now to things of more direct interest to mammalogists and epidemiologists. These I consider to be, among many items, (1) traps and technique used in capturing live mammals of all kinds in quantity, (2) documentation of the individual animal by means of an original record sheet or protocol, (3) growth studies, (4) data on movement of cebus monkeys by release and recapture of marked individuals, (5) temperature records, (6) collection of ectoparasites, and (7) problems arising from the work of scientific identification of the material and from the compilation of laboratory handbooks to

be used by investigators in gaining a basic knowledge of mammals for epidemiological research in South America. Such subjects as transportation, caging, feeding, bleeding techniques, field sterilization of instruments, preservation of specimens, the use of a dermestid beetle colony for cleaning skeletal material, and ecologic studies I shall deal with lightly.

The field studies were made under the auspices of the Cooperative Yellow Fever Service maintained by the Brazilian Ministry of Education and Health and the International Health Division of the Rockefeller Foundation.

TRAPPING LIVE MAMMALS

For trapping mammals (and other vertebrates) alive, four standard types of traps were adopted after much trial and error and invention. These were supplemented by a half dozen special types.

The requirements of the "live" traps were these: (1) *Efficiency*—they had to catch; (2) *durability*—they had to hold unusually strong and destructive animals and stand the wear and tear of transportation and rough use over long periods of time; and (3) *portability*—they had to be collapsible or dismountable, if large, for convenient transportation in quantity by any means whatsoever—horse, hand, or motor car. Along the trap line of a mile or more, actual man power was necessary to transport them.

The four types of live animal traps which were finally adopted for general use were (Pls. 1 and 2; figs. 1–3): (1) the small rodent trap, (2) a medium homemade screen-wire model; (3) the larger National Live Trap Company improved folding trap; and (4) an even larger dismountable homemade box trap for monkey catches on tree platforms. In addition, Bailey leg-hold traps, pit-traps, tin-can traps, trammel nets, and especially large pole traps were used.

Two of these four standard traps, the small rodent and the large box trap, have gravity fall doors; the other two, the medium screen-wire model and the folding trap, have spring-actuated doors. All, however, have the false-floor principle for a trigger. The animal does not have to take the bait; it just has to investigate far enough to get caught. A fifth type often used was the large pole box-type trap. It was made of stout poles, had a gravity fall door and false floor, and was constructed only in localities to be trapped for several months or more (see fig. 4).

It must be remembered that these four main types were in almost constant use daily, for months and even years. They were responsible for at least 75 percent of the 5,000–6,000 vertebrates captured in the course of the investigations, and thus are proven traps, not gadgets.

The most interesting trapping was for arboreal mammals—monkeys, porcupines, kinkajous, and certain rodents. Traps, principally the large demountable box-traps, were set on platforms in the trees at localities where passage of arboreal animals was most likely, or where evidence, in the form of corn-husks, indicated habitual depredations on an adjacent cornfield by monkeys. Cebus monkeys were the main catch, and were taken in quantity—126 in one locality in two years; 72 in another locality in eight months. Many cebus were also

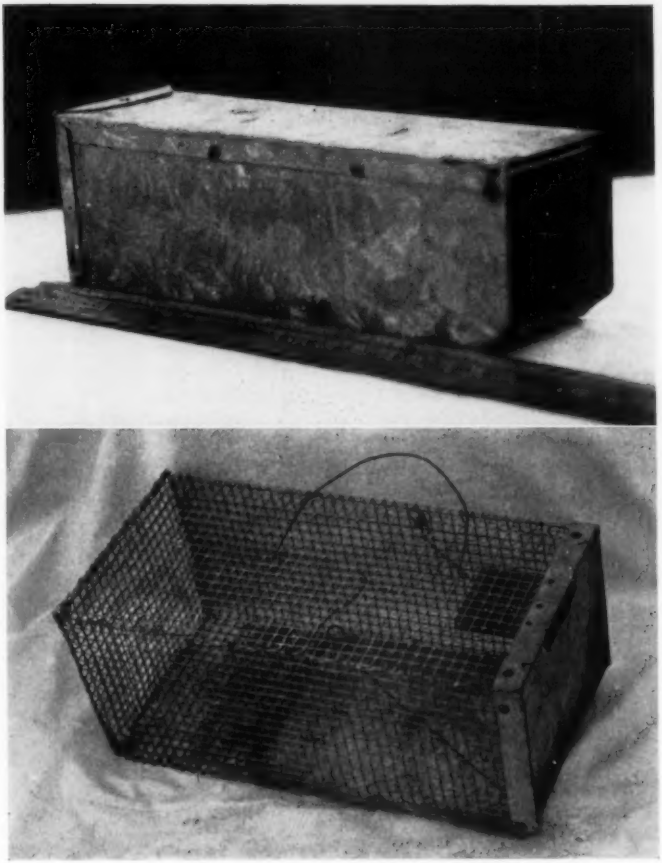

PLATE 1

UPPER: Small Rodent Trap. Galvanized metal. The top-hinged gravity-fall door connects to the false floor by a front right-angle arm of the latter. A gravity fall catch automatically locks the door when trap is sprung. The rear of the trap is for bait. Careful adjustments are needed on balance of treadle, catch, and trigger. The bottom-hinged back overlaps sides and top and is secured closed by a top friction catch. This is an ideal, sturdy, efficient trap for small rodents even if it does not collapse like the Sherman type. There are no springs to break or rust, and any damages are easily repaired anywhere. Manufactured by the National Live Animal Trap Co., Tomahawk, Wis. (For details of construction see fig. 1.)

LOWER: Medium Size Screen Wire Trap (home made). Galvanized screen wire. Door and flooring and front edge made of sheet metal. Door is top-hinged from within on a rat-trap base; and is locked by two gravity fall wire catches. Trigger wire connects door to false floor after a loop through roof. This is one of the most sensitive and efficient traps used in the work. Unfortunately not collapsible. (For details of construction see fig. 2).

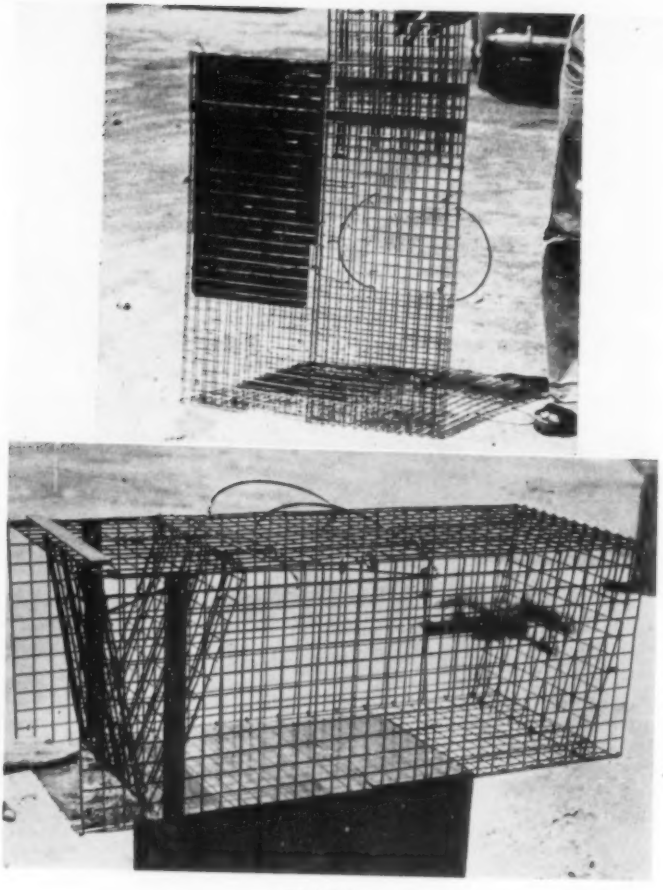

PLATE 2

UPPER: Improved Folding Model (in folded condition). Collapsed sides are held together by an attached hook. (See lower photograph of same trap set up for use.)

LOWER: Improved Folding Model, National Live Trap (Nat'l Live Trap Co., Tomahawk, Wis.). 32 x 12 x 12 inches; weight, 10 lbs.; soldered steel wire; spring-actuated door with bottom hinged counterpart which automatically locks door when trap is sprung. Improvements by special order are the metal flooring in front and steel reinforcements around mouth, both of which prevent a powerful animal from engaging claws in the front and forcing its way out around door. False floor connects to hook on side of door by two wires at right-angles to each other on one side. This efficient trap is collapsible. Seven or eight can be carried on a pack-board; whereas, if not foldable, 2–4 would be the limit for one man.

caught in ground traps. The surprising ease with which this monkey was trapped was due to its abundance, inquisitiveness, and dominating aggressive behavior. When individuals were accustomed to man, as they were around the cornfields in the sparsely wooded areas of southern Brazil, they rarely showed hesitation in entering traps to rob the corn and banana bait; and as many as three have been caught, on several occasions, in the same trap at the same time. In uninhabited areas, capture was not so easy, and time was necessary to accustom the monkeys to the traps.

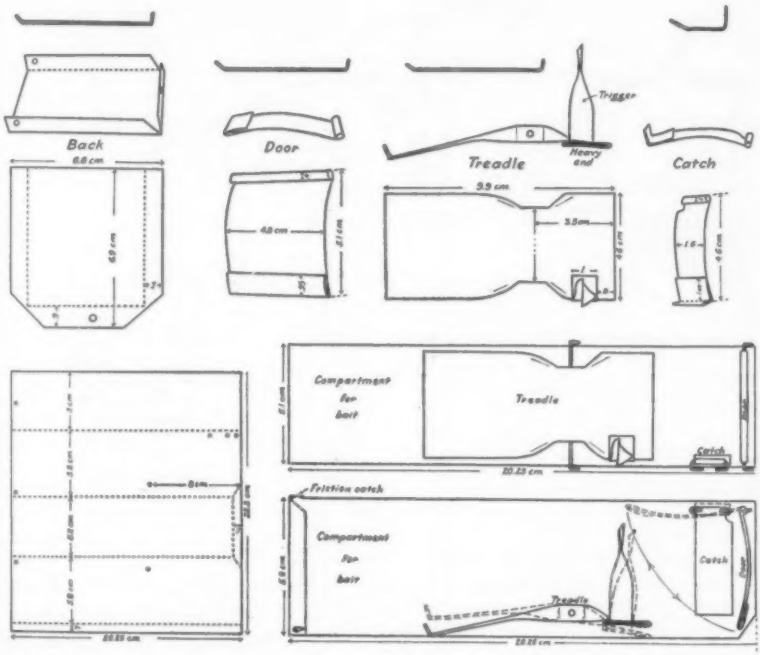

FIG. 1. Plans for construction of small rodent trap if one desires to make rather than purchase it (measurements in metric system).

Marmosets were also caught in some numbers. However, aside from cebus and marmosets, the only other monkeys caught were two howlers. Other monkeys were never taken in traps; but then, little trapping was done continuously on a large scale away from the planalto region of south central Brazil, which is inhabited only by cebus and an occasional band of howler monkeys.

Aside from these interesting aboreal catches, the other trapping was on the ground, and produced the usual run of many types of small rodents and opossums, with an occasional large rodent or small carnivore.

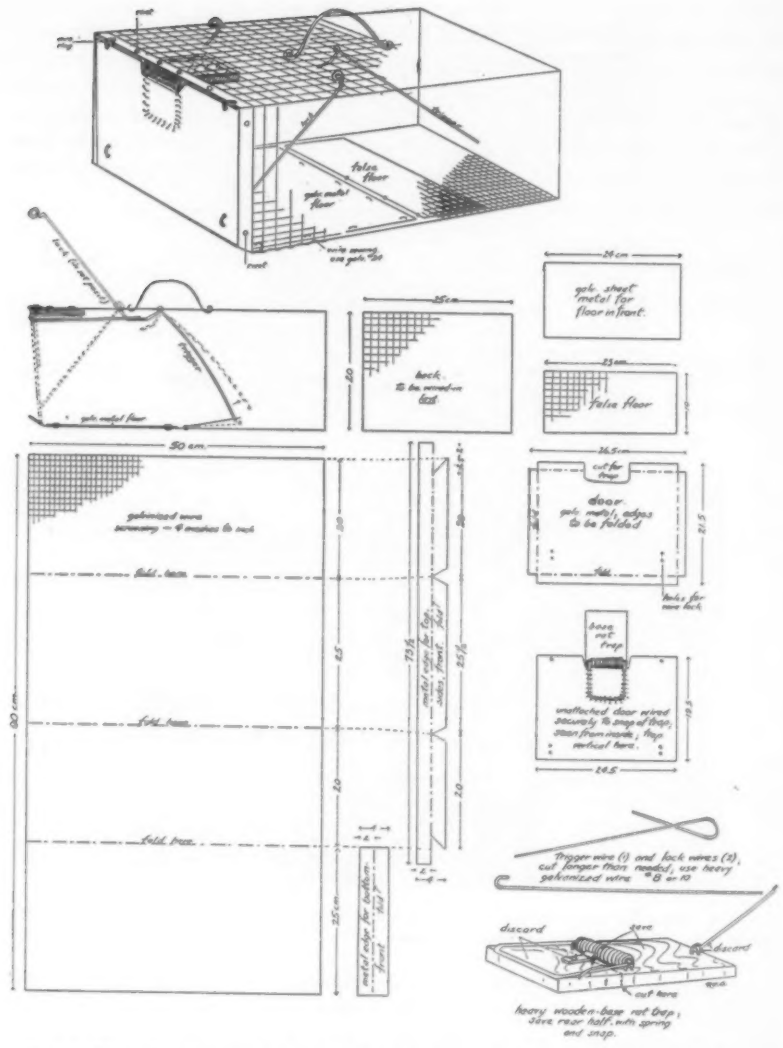

FIG. 2. Plans for construction of medium-size screen wire trap. (Galvanized screen-wire and sheet-metal, sensitive, efficient, light and strong. All measurements in centimeters.) Directions: (1) Fold screen-wire of body and sew at one edge with #24 galvanized wire. Use this edge for one side of bottom. (2) Place rims of metal around mouth and rivet. Bend up bottom front edge and overlap metal rims at sides and rivet. Mouth should be rigid and square. (3) Wire the prepared metal door to snap of rat trap so that it swings easily with no more clearance of coiled spring than necessary, and so that upper edge

RECORDING OF DATA

The second item of interest to mammalogists, and one which I believe to be of more importance, is the protocol record for the documentation of the data of each animal examined and bled. The word protocol has been adopted as the best English equivalent of the French *Protocole* and *Fiche de Documentation*, Portuguese *Ficha*, Spanish *Ficha*, German *Protokoll*. Rode (1937) discusses the

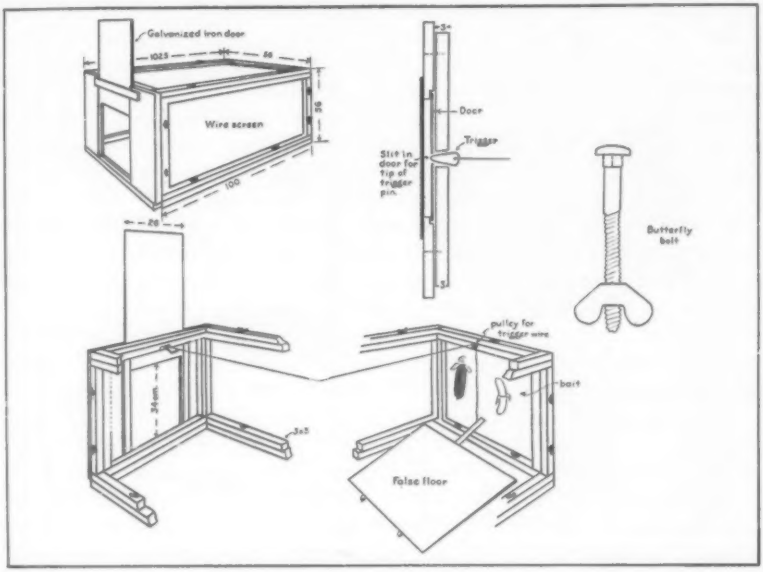

FIG. 3. Plans for construction of large demountable box trap. Door must be of metal to prevent swelling in wet weather. Frames of sections must be on outside when mounted to offer no wooden surface to animal for destruction (measurements in metric system).

value of such records in field work and gives a sample of one used by the Muséum National d'Histoire Naturelle, in Paris. This animal protocol, like the medical protocol, was a case history and post-mortem record of the individual, whether it was saved as a specimen or not. It was originally a short epidemiological

of metal door is ½ cm below and parallel to rat trap base when same is held at right angles to door. (4) Place door in position in body of trap with rat trap base flat against roof and flush with front edge. Mark position of holes (already punched through metal rim of mouth on top) on rat trap base. Remove, drill for screws, replace and attach securely by screws. (5) Fix and attach wire locks for door. (6) Hang trigger. (7) Put in false floor just beyond middle of trap. Test functioning of door, locks, trigger, and false floor. (8) Put in sheet metal flooring in front. This is necessary to prevent powerful animals from hooking claws through screen wire of floor and forcing the door. (9) Put on handle. (10) Sew on back, without altering squareness of front.

record of mammals bled for an immunity test; later it was developed into a more complete record for any vertebrate, and contained additional spaces for details of the structure, behavior, and ecology of the animal in order that we might know it better in the field. We had little knowledge of the vertebrate fauna to start with, and the literature was inadequate for field work. We had to learn the animals from specimens, living and dead, by examining and comparing

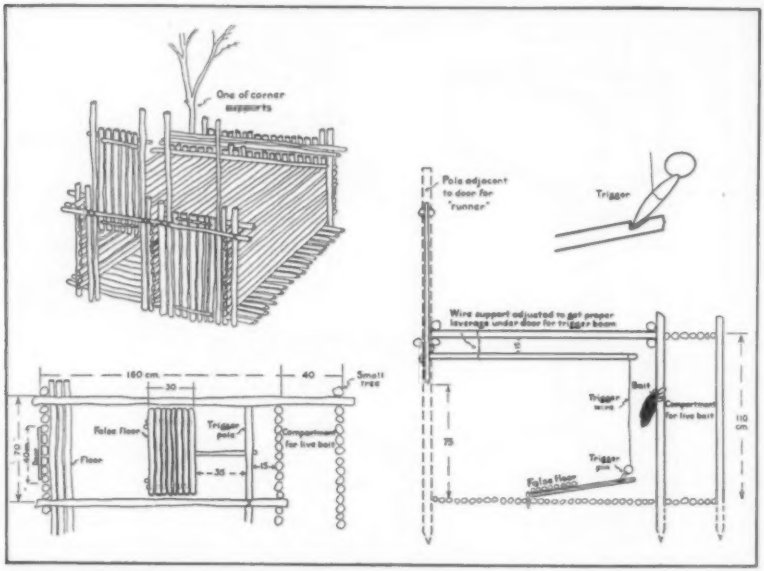

FIG. 4. Plans for construction of large pole trap (measurements in metric system). This is a solid permanent trap which can be neither demounted nor moved from the spot of construction. Hence it is justified only when large animals are desired from a locality to be occupied for at least 3–4 months, and only when a very favorable spot can then be found. Will catch and hold anything from agoutis up to peccaries, ocelots and giant maned foxes. Try to cut all the poles needed at first. Place corner posts, using a small tree for one; lay floor, then sides, back, door, trigger gadgets, and lastly the roof. If a live bait compartment is desired, and it is strongly recommended, cut the side poles long enough. Top poles must be removable from the outer edge one at a time to stir up recalcitrant victims, and to make repairs on the trigger, which will often be necessary.

them in detail; and soon we came to know each species by its morphology, behavior, ecology, and common name. This was necessary because we had to distinguish each species in the field, designate it consistently by the same common name, and thereby be able to tabulate our results, from time to time, according to species. A simultaneously functioning dermestid colony cleaned up skulls and skeletons, and enabled us to check our species, previously diagnosed on all the external characters we could find, on osteological characters as well. The

scientific identifications always remained a secondary matter in the field, though later on, when they were determined, the details on the protocols again proved of immense value and interest in giving more details than usual for the determination and definition of natural morphologic groups and units, and then identifying a name in the literature as applicable. Other important reasons for adopting a detailed protocol were that *many identifications had to be made from them alone*, as it was impossible to save every specimen collected; also, *certain of the data had to be correlated* later with those of clinical case histories and entomological captures to obtain a complete epidemiological picture in the locality.

This protocol required the collector to observe and enter data that were otherwise usually overlooked, but that were obtainable only on the living animal or the gross fresh carcass at the time and place of capture. As lately used (it has been changed several times from the original as drawn up in Brazil), the protocol for mammals contains the following primary entries: Common name, field number, scientific name, locality in detail, date, habitat and means of capture, sex, condition of genitalia, weight, measurements on unskinned body and skinned carcass, mammae, embryos, tooth count, age characters, age estimate, stomach contents, parasites, abnormalities, and disposition of specimen. In addition, there is occasionally such secondary information as notes and sketches on foot-pads, rhinarium, vibrissae of head and carpus, ear, genitalia, palate, skin glands, tail scales, temperature, mammae arrangement, rib and tail vertebrae counts, color of iris, behavior, etc. Further information can be added to the protocol later when the skin, skull, skeleton, or preserved carcass is studied in a laboratory.

The primary data were filled in for every specimen, but not the secondary details. These, in the form of lengthy notes and sketches, were made on the first few individuals taken, and on a few later selected ones of each species, in order to gain an adequate idea of sexual, age, and individual variation. Sketches were found to be best placed on an attached sheet of drawing paper or bristol board, so that they could be inked in then or later, and used directly for publication if so desired. Photographs were included, and as many as possible were taken in the field on fresh material. A tripod was always available, and it is now believed that a demountable copying stand, for photographing small objects, should also have been included in the minimum requirements for special accessory photographic apparatus.

It is to be noted that all this information was included on our last protocol only, and realized in its entirety only by myself. It was found to be somewhat complicated for non-professional vertebrate zoologists, although the scantier data that other collectors entered always were of value. Our conditions of work, involving field laboratories occupied for a long time, with cages for the live subjects and an ice box for the dead ones, were ideal for complete study of the specimens. The application of the protocol, for the recordation of complete and accurate data in the field, also thoroughly brought out the fact that such data are as important as specimens in the ultimate usefulness of the collection and its identification, and that mere numbers of specimens alone do not con-

stitute a successful field study. However, even with extensive protocol records, over 2,000 specimens were saved by all field parties over four years' time, and adequate series of most species were available for identification. A specimen was not considered as merely a skin and skull. Skeletons and salt-formol specimens of both sexes were also preserved; and, routinely, the long bones and scapula on one side, plus clavicle and baculum when present, were saved with the skull. A certain few common species were collected from the same locality in series of 50 to 100 or more in order to get key series that would include all age groups of both sexes. These key series with complete data are essential for an analysis of variation of a single population, for they enable the problem of subspecies and species to be better understood.

AGE GRADES OF MAMMALS

Previous studies of age grades of mammals were found to be rare, and such were not realized by us as early or as completely as they might have been. It soon became apparent, however, that by knowing the approximate ages of mammals at the time of capture and bleeding, the recentness of the occurrence of yellow fever in an area could be judged, if it had occurred at all. For instance, in dealing with a large number of the critical primate and marsupial blood sera from an area not represented by human samples, no immune samples might mean that there had been no yellow fever for many years (15 or so); immunity in samples from animals over 2 years of age only might indicate yellow fever present *up to* 2 years prior to collection; and immunity in all age groups would suggest that yellow fever was present at the time of collection and was perhaps endemic. A similar procedure is commonly used in analyzing collections of human bloods, with more accurately recorded ages. It is believed that *animal blood surveys on susceptible species in certain critical areas where it is impossible or exceedingly difficult to get human blood, can be used to detect the presence of jungle yellow fever.* At present this may have application in the movement of armed forces or the establishment of military bases in the tropics of South America or Africa.

Growth rates were determined both by direct and by indirect methods—although each depended upon some easily observable change in morphology such as tooth replacements primarily, and suture and epiphyseal closures secondarily. The tooth changes were of course the best, because they were observable on the living animal or discarded carcass; but unfortunately these changes are non-operative after maturity.

As an example of the method used in directly determining growth rates, the cebus monkey may be used. This animal is important because of its close, direct tie-up with jungle yellow fever, and its abundance. Ten different individuals were reared or retained in captivity and observed for periods of time ranging from six months to two years. Four more were born in captivity, probably prematurely, and soon died. The tooth counts and changes of all that had been noted were fitted together, and the following were the conclusions (the

species observed was the Tufted Cebus, like *Cebus fatuellus*, from Anapolis, South Goyaz, south central Brazil):

Infant 1 age grade (incomplete deciduous dentition): 1 to 6 or 8 months.

Infant 2 age grade (complete deciduous dentition): 6 or 8 to 14 or 18 months.

Juvenile age grade (mixed deciduous and permanent dentition): 14 or 18 to 36 or 40 months.

Subadult age grade (incomplete permanent dentition—sometimes an omitted stage due to replacement of milk canines *after* eruption of last molar, $M\frac{3}{3}$): around 36 to 42 months.

Adult age grade (unworn complete permanent dentition): 3 or $3\frac{1}{2}$ to 8 or 10 years (?).

Old adult age grade (worn permanent dentition): 8 or 10 to 15 or 20 (?) years.

The infant and juvenile age grades were further split up into time intervals by data on the replacement and eruption of individual teeth.

It is of interest to note that this scheme was worked out at the end of two years of study on the first nine live individuals, which did not include one born in captivity. The actual age in months and years of these first nine young cebus was indirectly estimated on breeding season data (young are born generally from September through December). But a tenth live specimen, taken on the mother's back when but two or three weeks old, and raised for 15 months, filled in the critical gap and gratifyingly confirmed the previously estimated ages of the later growth stages of the others.

An example of growth rate and age estimate by indirect methods (not rearing subjects for long periods for observations), is afforded by the white-eared common opossum (*Didelphis paraguayensis*) in Anapolis, S. Goyaz, S. C. Brazil. By way of necessary explanation, it must be stated that the didelphoid opossums pass through the following post-pouch age-grades based on tooth changes: *Juvenile*, with the only deciduous tooth, DP $\frac{3}{3}$ (the third in the jaw), still retained, and permanent M $\frac{1}{4}$ not erupted; *subadult*, with permanent P $\frac{3}{3}$, but still without M $\frac{1}{4}$; *adult*, with complete permanent dentition, I $\frac{5}{4}$, C $\frac{1}{1}$, P $\frac{3}{3}$, M $\frac{4}{4}$. Also of value is the information that *Didelphis* generally has two litters of young a year, about $3\frac{1}{2}$ months apart.

Information on 430 protocols and 206 specimens (from two localities; one for two years, the other for eight months) showed: (1) that females with young in the pouch were taken in seven consecutive months of the year; (2) that juveniles with deciduous P $\frac{3}{3}$, and subadults with permanent P $\frac{3}{3}$, appeared in the traps in two "waves" during the year; (3) that the juveniles appeared from four to eight months after the females had their first and second litters; and (4) that the subadults appeared from 6 to 10 months after the females had their first and second litters. Thus the juveniles were up to six or eight months of age; the subadults, 8 to 10 months old; and the adults, from 8 or 10 months on up to probably three or five years.

These are two examples of our growth rate studies. There was similar concrete information taken on many other mammals, but this has not been com-

pletely worked up. Complete growth rate studies are uncommon but important enough to make it seem advantageous for zoological gardens with a technical staff to study their live, or deceased and preserved captives, and thereby make substantial contributions to the subject, even though the data might be taken under abnormal conditions.

In presenting information on growth rates, it was found to be necessary to explain the development and change of dentition in detail and to include as many photographs as possible, because the teeth must be thoroughly understood in order to distinguish the deciduous from the permanent. Tooth counts and analyses are in reality difficult enough to require the observer to be a specialist in the matter.

For animals that show few, if any, changes in detition during growth, close analysis of suture and epiphysical closures and ossification of carpal and tarsal bones is necessary to determine age. This is also the case for the tooth-replacing animals *after* the last tooth eruption has occurred.

TERRITORIAL MOVEMENT OF CEBUS MONKEYS

The data on this subject were based on the release and recapture of marked individuals. About 50 cebus monkeys were tattoed and released, and at least half recaptured (some more than once, and one eight times). However, many of the results were rendered of less value than if the releases and recaptures could have been made consistently in reference to the home territory of the individual. It was often necessary to move the trap line some distance to other localities that appeared to be more important in the studies of yellow fever. Nevertheless, there were results of interest. We did find that most of the cebus were definitely territorial-minded, though some few did a great deal of wandering for one reason or another, natural or otherwise. The greatest accurately checked distance moved was 5–6 km. In several cases, in one locality, this distance was covered by cebus moving *out* of their home territory where they were originally trapped and released; in other and more cases, in another locality, a similar distance was traversed by individuals returning *to* the site of original capture, their home territory, from sites of release some distance away. More important than our inconclusive results, however, was the suggestion that this line of work is a very desirable one to carry out in more detail when conditions such as ours may be available to a mammalogist in the future.

The relation between animal movement and yellow fever is this: A phenomenon of jungle yellow fever is its movement, either by steady progression or jumps, from place to place. The character of jumping, sometimes a matter of scores or hundreds of miles, has not as yet been explained—it was at one time thought that birds, such as buzzards, carried the virus over long distances. The steady progression of yellow fever through a region, however, may be explained by contact of one population, band, or single animal with another near by, where conditions are favorable for transmission of the infection. But the speed with which yellow fever infection sometimes moved in this way suggested actual rapid and extensive movement of infected animals themselves. No vertebrate, however, has yet been incriminated as a traveling carrier.

BODY TEMPERATURES OF MAMMALS

Such information was considered of value, because laboratory experimentation on any animal for disease susceptibility (and many of the animals captured for a blood sample were so used later) generally involves consideration of the normal temperature in order to determine fever conditions. To obtain this basic information a temperature reading was taken on each live specimen as it was bled under ether. To render each reading as "normal" as possible, the animal was handled as little as possible. This means that it was never seized with the hands, nor excited unduly, unless absolutely necessary. Generally it was passed from the sack or cage, in which it had been brought from the trap line, directly to the ether jar. Large and unruly animals were passed from cage to sack, and etherized therein. Such technique also prevented injury to the animals, as well as wear and tear on the assistants' hands, both being important considerations. Also, to gain a better idea of normal temperatures, certain tame animals were sometimes tested for temperature without any excitation, etherization, or bleeding; and certain recently-captured wild animals were tested before, during, and after etherization and bleeding. Results showed no constant significant difference from regular readings taken under ether at bleeding, except in some cases where slight depression of temperature was noted several minutes after heavy etherization.

All temperatures were taken rectally, and were recorded in degrees centigrade. Insertion of the thermometer to bury completely the mercury bulb was far enough. For most mammals, an ordinary veterinary thermometer was used; but for other mammals whose temperatures were normally under 35°C., a special chemical thermometer was used. Those mammals which registered low temperatures, from 30–36°C., were sloths, armadillos, anteaters, and most opossums. The other mammals, bats, monkeys, marmosets, rodents, carnivores, and ungulates, registered from 36–39°C.

The temperature records were arranged as a list of readings, taken directly from the protocols, in a frequency distribution, so that the spread from mean to extremes was visible at a glance. Condition of taking was also noted.

COLLECTION AND PRESERVATION OF ECTOPARASITES

As yellow fever is an insect borne disease, and as jungle yellow fever is known to have a cycle *without* the domestic mosquito *Aedes aegypti*, an intensive search for any and every other possible insect vector was included in the investigations, and ectoparasites of vertebrates received attention. The collection of mammalian ectoparasites was done at time of bleeding for a serum sample. While the mammal was under ether it was combed and searched and the ether jar was inspected for every ectoparasite. These (all species and individuals found) were immediately placed together in alcohol in the same glass tube that contained a label inside with number and name of the individual host. The number was the same as the serum number, protocol number, and the number of the specimen if it was saved. The parasites were put in the tube between layers of cotton to prevent abrasion. Later each tube, filled with alcohol, was placed in a wide-mouthed Mason jar between cotton pads, and the whole jar was filled with alco-

hol. This prevented evaporation from individual tubes and subsequent desiccation of the specimens.

The bleeding and parasite inspection of each animal took place the day on which it was caught, and immediately after it was brought to the laboratory. Also, cages and sacks were washed frequently with lysol, and different species of mammal were not mixed together during transportation. These factors rendered the collection of ectoparasites as reliable as could be expected.

Dead parasites, to be sure, give only an idea of which ones infest certain animals. Actual transmission of yellow fever was tested on live batches of the parasites submitted to the experimental part of the field laboratory when it was equipped to handle this work.

PRESENTATION OF TAXONOMIC INFORMATION

This required special consideration because: (1) a selection had to be made of the mammal groups, a knowledge of which would be of most use to the yellow fever laboratories, and (2) the presentation of this information had to be done in such a manner that understanding would be complete for the non-professional mammalogists in the laboratories and the field.

Results of immunity tests showed that the mammal groups most intimately connected with jungle yellow fever were Marsupialia and Primates. Hence, these two orders were subjected to a more thorough study than the rest, and a handbook for field identification was drawn up for all the South American representatives of these two groups. These, and other vertebrates, were represented by about 6,000 laboratory protocols, and about 2,500 specimens, of which about 2,200 were mammals; 250, birds; and 50, reptiles and amphibians. One and one-half years were assigned to the task of identification and writing.

The American Museum of Natural History in New York, by invitation of Dr. H. E. Anthony, Curator of Mammals, kindly offered its facilities of good comparative material and complete library service. Here the birds were turned over to Dr. J. T. Zimmer, and the reptiles and amphibians to Drs. H. Bassler and C. M. Bogert. To all these men, especially the latter two, who gave much of their time, sincere acknowledgment is hereby made for assistance rendered. The mammals remained with the writer.

It immediately became apparent in the presentation of the taxonomic information, that certain principles were to be observed to keep misunderstanding and misidentifications at a minimum for the laboratory or field worker. These were: (1) The subgroups (families, genera and species) of the orders involved must be discussed in their entirety. Relationship and relative degrees of differences plus total ranges are essential for the understanding of any species, genus, or family. Very few papers on mammalian taxonomy, even written by professionals, are complete in any of these respects. (2) Clearcut definitions of scientific names must be established before the names are used in an absolute sense.

To accomplish these ends, the following outline of presentation was adopted, and the following parts included: (1) The best English vernaculars, and all

known indigenous names; (2) a complete diagnosis with definition of all the salient characters; (3) a list of the most important synonyms; (4) as many illustrations as possible, in the form of photographs and sketches; (5) total number of specimens examined or recorded in the literature, and their localities; and, (6) the original description of the species, with original illustrations sometimes photostated (this gave the real reason for using the names). All changes from the generally accepted classification and nomenclature were explained, and the reasons given. Also, those forms that could not be classified easily were listed as of indeterminate status; no attempt was made to clarify the taxonomy by omitting or falsely simplifying the difficult parts.

No keys were used because it was found that animals were better understood, for the uninitiated, through a knowledge of all their salient characters, made evident in the form of a diagnosis. A key emphasizes but one or two characters which may be obscure or unimportant, while a diagnosis defines the animal as a whole, which is what it is. In making these diagnoses, the protocols were of special value (in addition to their original purpose of species discrimination in the field), because they gave reliable first-hand information on the morphology of the soft parts, on weights, temperatures, etc. These data are those most frequently unrecorded and hence generally unknown, but often they are as important as the standardized osteological, size, and color characters taken from the usual skin-and-skull-only specimen, and nearly always more valuable in field identification. The photographs of the living or dead animal and the sketches of the anatomical features were, of course, as valuable.

It proved well worth while, therefore, from more than one standpoint, to spend time in the field on a detailed study of the living or freshly dead specimen.

The importance of standardized common names also became evident. Experience in the field had showed conclusively that a knowledge of indigenous names for mammals was of immense value for local communication and experience with technical reports indicated that sensible, oft-used English equivalents for groups and species were often more definite than the scientific names. Hence, every effort was made to include all known local indigenous names and to use standardized English vernaculars. When such English vernaculars were absent or numerous and highly variable, one was invented or selected, but only after a knowledge of all related groups and species had been gained, so that there would be no confusion in the meaning and use of the adopted name.

Due to the mass of scattered incomplete literature on South American animals, and the very large collections in the American Museum of Natural History (for example, about 800 *Cebus*, 525 *Alouatta*, 1,000 *Proechimys*, etc.), specimens came first in the studies, and the literature second. But an effort was made to consult all the best and most complete papers and all the original descriptions. Identification by locality, *e.g.*, the use of the name of the geographically nearest described and most closely related animal, without regard to the validity of the name in the face of the actual structure of the group, was not done when there was time to analyze the morphologic structure of the whole group.

Likewise, mere variation, without regard to its relative value or weight in its own group, was not emphasized.

An incomplete example of this procedure in taxonomic presentation was attempted in a report on the marsupials of eastern Colombia (Bughen, Boshell, Roca, and Gilmore, 1941). Here it is believed that the method used leaves no doubt as to the actual identity of the animals involved.

TRANSPORTATION, CAGING, FEEDING, BLEEDING, STERILIZATION, PRESERVATION OF SPECIMENS, ECOLOGIC STUDIES

These subjects will be outlined only briefly. A complete discussion would occupy many pages and require many figures.

Transportation was done from trap line to laboratory in tandem screen-wire portable cages with sliding and lockable doors, or by sacks. Cages were better than sacks because ventilation was better, but they were bulky and for the larger animals sacks were the rule. Sacks are efficient for imprisoning animals because most species do not attempt to chew or claw out of yielding walls in the dark. Cebus monkeys are, however, an exception to this rule.

Caging was done in a variety of cage types, but all were designed to provide room for some exercise and a nest box, and the doors were so made that placement and extraction of the animal was most efficient, and escapes were at a minimum. One large vivarium for many cebus monkeys was constructed and served well; tandem shelter boxes with sliding doors on a raised platform were also used for catching and sorting monkeys. Whenever possible, ordinary cages were collapsible or were made in demountable sections to facilitate transportation.

Feeding involved utilization of what the local supply had to offer, but variety of type and regularity of time were two principles observed. Bananas and corn kernels were the principal items, with meat scraps, whole mice and rats, sugar cane, milk, eggs, and cooked rice and potatoes supplementing. Certain few animals required special diets, such as termite ants (in the mounds) for anteaters, and a milk-egg-chopped meat-cooked rice ration once each evening for nine-banded armadillos.

Bleeding for a serum sample was generally done from the heart, except on larger forms where the femoral artery was utilized. All subjects were bled under ether, and the trauma of puncture, when this was properly and quickly done, was rarely severe enough to cause death even in rodents and marsupials of a weight as low as 25 grams.

Sterilization of syringes, needles, tubes, ampules, pipettes, etc., was done exclusively in a Pasteur dry sterilizer. Syringes were wrapped in especially tough but thin paper, needles were placed in cotton-plugged glass tubes, glass tubes for blood were stoppered with cotton and left uncovered, ampules likewise, and pipettes were plugged at the mouth-end with cotton and placed in copper containers. All were subjected to 170°C. for 20 to 30 minutes, then 150°C. for another half hour. Higher temperatures char paper and cotton. Heating was done with a gasoline primus stove. The sterilizer was demountable.

These instruments remained sterile when placed in proper containers, and hence were ready for use on an instant's notice. Contaminations were less than 1 percent, and were not always due to the condition of the instruments.

The preservation of a proper number of desirable mammal specimens for identification was done in such a manner that the least amount of time was spent in insuring a perfect and permanent result. Small species were made up into study skins on the spot; larger ones were dried *in shape*, hair side out, and then wrapped in strong paper with paradichlorbenzine crystals. Both large and small types were disinfected with carbon bisulfide or carbon tetrachloride gas before wrapping or packing away with crystals of repellent; and both were always thoroughly cleaned of grease and dried as preliminary steps. By these means, no losses from insects, molds or fat burns were experienced.

The skulls and skeletons were dried and cleaned at once by a colony of dermestid beetles that was carried around in a wooden gasoline case provided with trays and a tight lid. In this way nearly all cranial and skeletal material was cleaned in the field, and there also boxed or vialed. The amount of help this conferred upon subsequent treatment of the collection for study in a museum may well be realized. Cheesecloth sacks separated specimens in the bug box; tags were of lead, aluminum, or imitation (treated) parchment paper only; bugs eat true parchment along with the flesh of the specimen.

In extremely wet weather, especially during continual dampness, artificial heating was used to dry skins and skeletal material, and keep the dermestid colony going.

For pickled whole specimens, a solution of saturated salt—2 percent formol was used. This preserves well, without stiffening the material, and is devoid of the usual irritating formol odors.

The preservation of specimens for absolute identification in public health investigations is generally an acute problem, because trained field zologists are often absent, and because the technique is a special one. With this in mind it is suggested that the documentation of every specimen by a protocol, with a few skins temporarily preserved by thorough drying in shape and the saving of even skulls of *every different recognizable kind, designated consistently by the same common name*, will enable identifications to be made at a later date with a certain amount of surety. A bug box, functioning in the field, will permit identifications, or at least the distinguishing of different types, to be made on the spot. It is extremely important to recognize every different kind of mammal in the field, no matter how obscure its characters may be; and then designate it consistently by the same common name, borrowed from the local inhabitants or invented. Instances of confusion have often resulted from failure to observe these principles of close identification and consistent designation in the field.

The biologic and ecologic studies included, besides the mentioned growth rate, territorial movement, temperature, and parasite studies; also the data on relative abundance, habitat, and any factors that have direct relation with the mammal and a possible insect vector, especially the mosquito. The trapping

activities, organized by ecologic associations and run morning and evening, and the retention of animals in captivity, with the use of some for mosquito bait, were the main lines of activity to provide such data. This work can be concentrated and augmented on certain species when these, by a high percentage of immunity in yellow fever areas and by a specific susceptibility in the laboratory, show that they are probable hosts.

In conclusion, I wish to say that all these discussions of techniques, procedures, and summarized results have been intended primarily to show how mammalogy, on this occasion, was specifically fitted into a medical research program. Working with the usual knowledge of morphology and natural history of mammals, specimens were caught alive, bled, tested for temperature, examined, caged, released and recaptured, marked, reared, and saved as studiable specimens with complete data. It is hoped that these applications may be of interest to the pure research mammalogist.

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NOTES ON THE BREEDING HABITS OF THE EASTERN FLYING SQUIRREL (*GLAUCOMYS VOLANS VOLANS*)

By Dwight E. Sollberger

Detailed information concerning the breeding habits of the eastern flying squirrel (*Glaucomys volans volans*) cannot be found in the literature. Sufficient data have accumulated to show that more than one litter may be produced each year, but considerable disagreement still exists on even this fundamental phase of the animal's life. Audubon and Bachman (1846, p. 218) mention having seen young in May and September. Langdon (1880, p. 23) observed a litter with eyes unopened on September 7. Wood (1910, p. 535) says that they are said to produce a single litter each year in the north, but as many as three in the south. Evermann and Clark (1920, p. 478) observed litters in April and August. Howell (1918, p. 8) concludes that a second litter may be produced in August or September. Brimley (1923, p. 263) records litters for September and March in North Carolina. Various other writers are of the opinion that only one litter is produced each year.

The present study shows that one mating takes place in late February or early March, and another in July. The evidence for the time of breeding was based on litters taken under natural conditions, gravid females collected under natural conditions and later bearing their young in captivity, embryos taken from trapped females, and nursing females that were collected. No females mated more than once during a year in captivity (Tables 1 and 2). Early in the study it was learned that the eyes of the young opened 28 days from the time of birth. It was also learned that the period of gestation is 40 days. With this information it was possible to approximate closely the date of mating when a litter with unopened eyes was collected. By this means it was estimated that of a total of 24 matings known to occur under natural conditions, 12 took place in February, 9 in March, 2 in June, and 1 in July. In addition, 11 nursing females were collected on the following dates in 1937: September 12, September 16, September 19, September 22, and October 5. One female with four embryos was taken on September 14, 1937. Since only 13 females in all were captured, and eleven of this number were nursing, the assumption that a second mating occurs in July seems justified. The young of a spring mating were observed to shift for themselves after six weeks of nursing. At this time they were able to develop to maturity when removed from the parent, although in the natural state I observed considerably older animals with the parent. The length of the period of development does not preclude a third litter, but I have no evidence that such is the case.

Two captive females were observed to be in heat in July, but no litters resulted in either case. One party in East Palestine, Ohio, from whom I purchased a pair of flying squirrels, stated that the male of the pair was one of a second litter born in September. The first litter was born in April. Testes of captive flying squirrels descended in late January and early February, and were retracted in September. Wild males with testes descended were taken from early March until September.

REPRODUCTION

Oestrous.—One female was taken showing the characteristic signs of oestrous. Thirty-nine days later this female gave birth to a litter of two. Ten captives were observed to come into heat during 1936 and 1937. Six of these females mated and bore litters. One was kept from males in order to make vaginal smears, and three bore no litters. Three litters were born in the spring of 1936 and three in the spring of 1937. The time of oestrous, mating, parturition, and the period of gestation are summarized in Table 3.

Oestrous can be recognized in flying squirrels by the changes in the appearance of the external genitalia. For the greater part of the year the opening of the vagina is closed by a membrane. The parts are flesh-colored and flaccid. Only a faint line marks the suture that will open when the animal is in heat. As the time of oestrous approaches, the lips of the vulva swell until they are approximately five times their normal size. The vulva becomes a reddish pink. When the swelling reaches its maximum, the lips part spontaneously to form an opening about 4 mm long. Six females in this condition mated and bore litters. Vaginal smears showed a large number of cornified epithelial cells. One female that was perforate was kept from the males for the purpose of taking a series of vaginal smears to learn the nature of the period if the animal were not allowed to mate. In this female the swollen and turgid appearance persisted for five days and then subsided for eleven days. At the end of this time the swelling again became evident, and cornified epithelial cells were again noted. During the period of decreased swelling cornified epithelial cells were greatly reduced in number. When the swelling was most prominent, the vaginal smears were almost opaque, and it was not necessary to stain the cells to see the difference. Following the second period of swelling all signs of oestrous disappeared and did not reappear until one year later in the spring of 1937. This female then mated and bore a litter. Further study of the oestrous cycle was discontinued due to the difficulty of securing a sufficient number of female squirrels.

After mating, the enlarged condition of the vulva gradually disappeared. This required from five to eight days. The perforate condition persisted for four to five weeks following parturition.

In the males the testes of some captives appear descended or partly descended throughout the year. The testes of wild males taken in October, November, December, and January were not descended. No males were taken in February, but males captured from early March until September had descended testes. More than a month of variation was noted in the retraction of testes of captives.

Courting and mating.—Kelker (1931, p. 166) observed under natural conditions a pair of flying squirrels in amplexus on March 12, 1930. I have not observed flying squirrels mating under natural conditions. Under captive conditions, male flying squirrels respond quickly to the presence of a female in heat. A female placed in a cage with several males was pursued almost immediately. She did not respond to their advances, but kept several feet distant. Occasionally a male would vibrate his hind quarters up and down very rapidly and kick backwards with a rapid motion of the rear legs. This was done when the female

was two or three feet away. The female squealed when approached and ran away. This behavior was continued for an hour with interruptions for feeding. After more than two hours had elapsed, an attempted mating took place, but the female did not appear to accept the male. The animals were allowed to be together over night, and in the morning abundant spermatozoa in the vaginal smear showed that mating had taken place. The gestation period was dated from this mating until partus.

Behavior during pregnancy.—During pregnancy, captive and wild squirrels became more tame and allowed considerable handling without biting. Their movements were not so quick and vigorous as were the movements of non-pregnant females. No differences in gliding ability were noted when gravid females were being captured, although conditions for accurate observations were never favorable.

The young can easily be felt two weeks before parturition by palpation. The body and hair of the animal are soft, and the stomach, full bladder, intestine containing feces, and backbone can easily be identified from the ventral side. Detection of gravid females in this manner simplifies the housing of large numbers of the animals, because such females may be kept with the others until near the time for the arrival of the young. They should then be placed in a separate cage.

DESCRIPTION OF YOUNG

Birth.—The young at birth (fig. 1) are naked except for mystacial vibrissae and very short hairs along the upper and lower lips. The color is dark pink. The patagium between wrist and ankle is very noticeable. Very small claws are present. The external ear is folded over ventrally and has no opening. The large eyes are visible as dark spots with faint suture lines marking the future openings. The scrotum is plainly visible in the male.

The movements of the young at this time are not coordinated. The rear parts of the bodies especially seem to be helpless. When placed on their backs on a smooth surface, they are unable to turn over on their bellies. When on their bellies, they have difficulty in staying there, tending to fall over on their sides. The young at this time move continually with a squirming motion and emit faint squeaks.

The weights and measurements of ten young at birth representing four litters follow:

NUMBER OF YOUNG IN LITTER	COMBINED WEIGHTS*	INDIVIDUAL WEIGHTS
	grams	*grams*
3	9.1	3, 3, 3.1
2	10.5	5.2, 5.3
3	10.7	3.5, 3.5, 3.7
2	6.0	3, 3

* These weights were taken after the young had sucked.

The average number of young from 24 females that mated under natural conditions and bore their young either in captivity or under natural conditions

was 3.1 per litter. Six captive flying squirrels produced an average of three young.

One week.—The head, dorsal part of the body, and tail are darkly pigmented (fig. 2). Hair is present on the head and neck. The ventral portions of the body are lightly pigmented but no hair is present. The patagium is flesh-colored. The conchae of the ears are no longer folded over, but no ear opening is visible.

Two weeks.—The body, except for the abdomen, is almost completely clothed with hair (fig. 3). The ear openings are marked by deep fissures, but are not yet open. Vibrissae are present on the fore legs as well as on the facial region. The under side of the chin and thorax is covered with white hair, and the back is assuming the color of the adult. The under side of the patagium, inner side of rear legs, and posterior portions of the abdomen are naked. The lower incisors are barely visible.

TABLE 1.—*Average measurements of young flying squirrels at various age levels*

AGE	TOTAL LENGTH	LENGTH OF HIND FOOT	LENGTH OF TAIL	WEIGHT	NO. AVERAGED
	mm.	*mm.*	*mm.*	*grams*	
At birth	62.1	7.2	15.8	3.63	10
One week	77.1	11.2	25.6	7.3	6
Two weeks	101.4	15.1	37.6	13.2	6
Three weeks	117.8	17.2	42.1	19.2	6
Four weeks	143.0	22.6	62.1	26.2	6
Five weeks	170.1	25.1	70.7	33.1	6
Six weeks	187.4	28.8	79.8	36.8	6
Eight weeks	211.0	31.0	96.0	44.5	1

Three weeks.—Hair is present except on the under side of the patagium, inner surface of the rear legs, and posterior parts of the abdomen (fig. 4). The ear opening is established. The movements of the animals are much more coordinated, but they do not move about freely, being unable to support their bodies for more than a few seconds.

Four weeks.—The eyes usually open at 28 days (fig. 5), varying from 26 to 29 days. The body is completely covered with hair. A darker band appears along the lateral edge of the patagium. The animals move about freely in the nest box, but do not come out. They were not seen to feed themselves at this time. The lower incisors are eight millimeters long, but the upper incisors are less than one millimeter long. The tail is eight millimeters wide. No attempts are made to jump or glide. When thrown in the air, they spread their feet and open their patagium, but they do not have the ability at this time to change the direction of the fall.

Five weeks.—The young at this time resemble the adults as regards coloration. The lower and upper incisors are developed sufficiently to enable soft foods such as nut meats to be eaten. Possibly in the wild state they continue to nurse and eat such soft foods as insects and succulent twigs and flower buds. They are active, coming out of the nest box and running freely about their cage.

Six weeks.—At this age the young seem able to take care of themselves (fig. 6). Unbroken nuts are not eaten, but nut meats, apple, and cow's milk are taken.

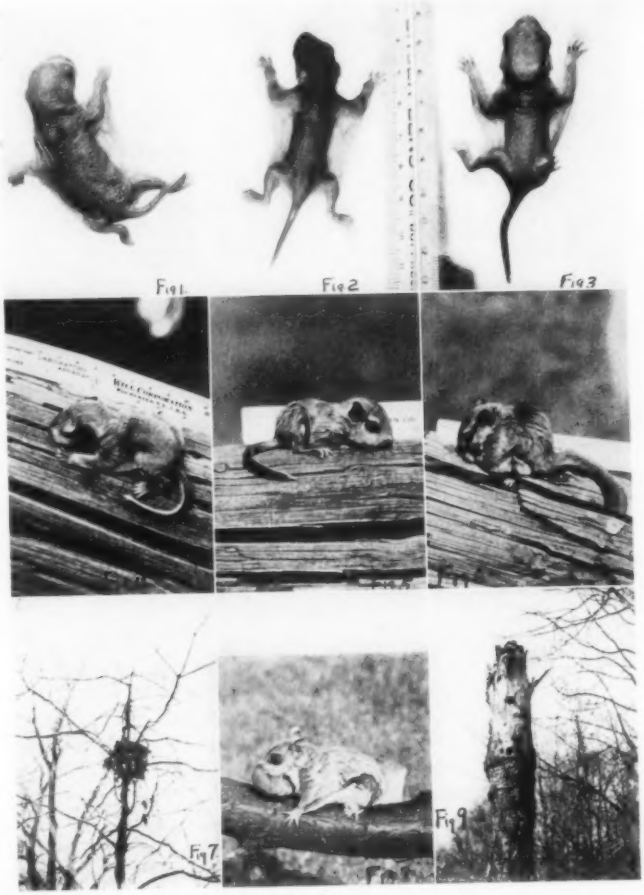

PLATE 1

Flying squirrel young, (1) first day; (2) 7th day; (3) 14th day; (4) 21st day; (5) 28th day; (6) 42nd day; (7) Outside nest of flying squirrel in dogwood tree; (8) Flying squirrel female carrying young; (9) Large-toothed aspen from which flying squirrel litter was taken.

The young are weaned gradually and begin eating solid food while still nursing. Young separated from the female at this time are able to develop to maturity.

Eight weeks.—The young were separated from the female and placed in a cage with other adults. They were able to care for themselves.

The following spring one female of this group bore young. Later litters matured by the spring of the following year, and both males and females were observed to be sexually mature. No summer broods were observed to determine whether they reached sexual maturity the following spring.

CARE OF THE YOUNG

From the time of their arrival until the fifth or sixth week, young flying squirrels are protected from danger by a mother whose instinct for protecting her young causes her to disregard anything but their welfare. On at least four

TABLE 2.—*Wild females with litters*

DATE OF CAPTURE	NUMBER OF YOUNG	AGE OF LITTER[1]	DATE OF BIRTH	DATE OF MATING	LOCALITY
1934		*days*	*1934*	*1934*	
April 8	4	8	April 1	February 22	Aliquippa, Penna.
April 16	4	14	April 2	February 25	Aliquippa, Penna.
May 1	3	3	April 28	March 11	Aliquippa, Penna.
August 25	4	40	July 16	June 7	Aliquippa, Penna.
August 17	3	4	August 13	July 4	Aliquippa, Penna.
1935			*1935*	*1935*	
April 19	4	12	April 7	February 27	Wooster, Ohio
April 19	3	7	April 12	March 12	Wooster, Ohio
April 20	3	28	March 23	February 11	Wooster, Ohio
April 7	3	2	April 5	February 26	Aliquippa, Penna.
April 14	4	9	April 5	February 26	Mercer, Penna.
April 14	4	6	April 8	March 1	Mercer, Penna.
April 1	3	7	March 24	February 16	Aliquippa, Penna.
April 27	1	23	April 4	February 27	Mercer, Penna.
May 6	4	27	April 9	March 1	Aliquippa, Penna.
April 27	3	28	February 27	February 19	Mercer, Penna.
May 4	1	20	April 14	March 6	Aliquippa, Penna.
April 30	2	30	April 1	February 19	Aliquippa, Penna.
April 5	4	19	March 17	February 6	Aliquippa, Penna.

[1] Based on the time they opened their eyes.

The average number of young per litter was 3.1.

occasions, I have captured nursing females by holding a young squirrel in my hand and imitating the sound of a young squirrel in distress. The mother will not only come to investigate, but will climb over one's hands with great indifference to her own welfare.

When they are younger, the female hovers over the young like a hen over chickens. She spreads her patagium by turning her front feet inwards. The young contribute to the spreading by pushing outwards from beneath. Usually the young feed in this position. At other times the mother lies on her side or even on her back while the young take nourishment. All mammae are used even though the litter numbers only two or three.

The male flying squirrel does not share the duties of parenthood, although

Seton (1929, p. 377) seems to think they pair. Males have been found within 100 feet of a female with a litter, but never in the same tree or nest. I have found at least 35 litters, and in no case was a male present at the time. Captive females have been kept with the males within a week of the time when the young were due without any sign of disagreement. Captive males placed within a cage containing a young litter were killed by the female, but young ones approximating the age of the litter she was nursing were cared for solicitously. Young white rats with unopened eyes were taken in and cared for by one female with a litter.

NESTING SITES

Flying squirrels seem to prefer holes in stumps to outside nests for purposes of rearing young. Although I have endeavored constantly to rout a flying squirrel with a litter from outside nests during this study, it was not until the spring of 1940 that a female with a litter of four was located in an outside nest. During this time more than 35 females with litters were found in holes in trees. There seems to be little choice of the kind of trees used for this type of nest. Nests were found most often in large-toothed aspen trees, but this was undoubtedly due to their being more often riddled with woodpecker holes. Females with litters were taken from holes in black oak, hemlock, red maple, black locust, apple, beech, chestnut, wild black cherry, basswood, and red oak trees. The only requirement seems to be that the opening be large enough for the squirrels to pass through it successfully. In addition the hole inside the tree must be large enough to provide room for some shreds of inner bark and the animal itself. In some cases the holes were scarcely large enough to conceal the flying squirrel, and wisps of fibers could be seen projecting out of the hole. A hole one inch in diameter is large enough to admit an adult flying squirrel. Larger holes would be advisable if one were to construct nest boxes for these animals. Under natural conditions the holes are usually one and a half to two inches in diameter.

The nest is always lined with soft material composed of the fibers of inner bark. This material stays soft and does not mat even when slightly damp. Captive animals quickly line their nests with this material when it is placed in their cages. This is done by both males and females. The young are hidden deep down in this material and one has to look carefully to discover them after the female has been captured or routed from the stump.

The stumps in which nests are found are usually quite old. This is probably not a requirement of the flying squirrel but of the woodpecker making the holes in such stumps (fig. 9). In many cases they are so badly decayed that they may be pushed to the ground with little difficulty. If living animals are desired, it is better to allow the stump to stand and use live-traps on the stump; otherwise the female will not return when the young have been removed.

The literature lists several observations of flying squirrels in outside nests, although I found no record that the construction of an outside nest by a flying squirrel has ever been observed. Flying squirrels were found in outside nests

on three occasions during this study. On one occasion the nest contained an adult female with four young approximately one week old. The two nests not containing young were located 24 feet and 20 feet from the ground in tangled grape vines. The nest containing the litter was 17 feet from the ground in the crotch of a flowering dogwood (fig. 7). The nest containing the litter was found in the spring and the other two were found in September and November.

The nests were similar to other squirrel nests in construction. The outer surface was composed of leaves and small twigs with leaves attached. The

TABLE 3.—*Females mated under natural conditions with young born in captivity*

DATE OF CAPTURE	DATE OF PARTURITION	NUMBER OF YOUNG[1]	DATE OF MATING	LOCALITY
March 20, 1934.....	March 25, 1934	5	February 14, 1934	Aliquippa, Penna.
April 2, 1935.....	April 13, 1935	2	March 5, 1935	Aliquippa, Penna.
April 5, 1935.....	April 8, 1935	2	March 1, 1935	Aliquippa, Penna.
July 21, 1935.....	August 5, 1935	3	June 27, 1935	Allegany State Park, New York
April 15, 1936.....	April 30, 1936	4	March 22, 1936	Ithaca, New York
April 18, 1936.....	April 19, 1936	2	March 11, 1936	Ithaca, New York

[1] The average number of young per litter was 3.

TABLE 4.—*Summary of the breeding records of ten captive flying squirrels*

NUMBER	DATE OF OESTROUS	DATE OF MATING	DATE OF PARTURITION	PERIOD OF GESTATION
				days
1	February 29, 1936	February 29 or March 1, 1936	April 9, 1936	39–40
2	March 13, 1936	no litter	———	———
3	March 5, 1936	March 5, 1936	April 14, 1936	40
4	April 10, 1936	April 10, 1936	May 19, 1936	39
5	July 21, 1936	no litter	———	———
6	March 15, 1937	March 15, 1937	April 24, 1937	40
7	March 16, 1937	March 16, 1937	April 25, 1937	40
8	March 28, 1937	March 28, 1937	May 6, 1937	39
9	March 28, 1937	no litter	———	———
10	April 2, 1937	no litter	———	———

inner portion was composed of a dense mass of shredded inner bark. The size seems to be smaller than the nest of the gray squirrel, but I was unable to observe significant differences in size due to lack of sufficient nests. As a matter of fact, I am not certain that the flying squirrel nests were not deserted gray squirrel nests. General observations from the ground support the belief that there are two types of nests that could be constructed by gray squirrels and flying squirrels respectively. The larger nest is certainly built by the gray squirrel and is more leafy in appearance. The smaller nest, which is presumably built by the flying squirrel, is more compact. The larger nests are more often located on branches

and crotches of large trees at greater distances from the ground. The smaller nest most resembles the nest of the red squirrel, but in the area where both types of nests were found the red squirrel had been exterminated. The construction is essentially the same. Differences in size were difficult to measure because of the loose, leafy nature of the material. Until flying squirrels are observed building nests, or until a large number of nests are found containing flying squirrels, the question of nest-building by flying squirrels will not be settled. That flying squirrels will take over the nests of birds and other squirrels is unquestioned. I have found flying squirrels in old bird nests, bird houses, gray squirrel nests in stumps, old cupboards, and attics. On one occasion gray squirrels and flying squirrels were dislodged from a stump on two successive days. I have never observed flying squirrels to carry material other than the fine shredded inner bark used to line their nests. It seems difficult to believe that these rather delicate animals can successfully carry the material found in the outside nests.

NUMBERS PER UNIT AREA

Seton (1929, p. 376) observed three nests of flying squirrels in less than an acre, and concluded that flying squirrels are more numerous than red squirrels in areas suitable to both.

This is also the belief of the writer. Two areas were trapped sufficiently to yield data on this point, but neither area was trapped to extinction. The first area borders the side of a slope along Raccoon Creek near Aliquippa, Pennsylvania. No part of the woods was less than 250 feet from the creek. The area was nearly rectangular in shape, measuring 550 feet in length and 300 feet in width, thus having an area slightly less than four acres. One side of this area was bordered by a road and a cultivated field, the second by some cut-over land that had grown up in brush, the third by a field grown up with hawthorn, and the fourth side sloped sharply to the creek level, the bottom being marshy and containing only a few small trees.

By means of live-traps and pounding on stumps, 19 flying squirrels were taken from this area, thus averaging nearly five per acre. As was mentioned above, this area was not trapped to extinction since the notes of those remaining could be heard at night.

At Ithaca, New York, 22 flying squirrels were taken from a portion of the woods near the Cornell University Rifle Range. The section from which the squirrels were taken was estimated to contain ten acres. This would give an average of 2.2 squirrels per acre.

DEGREE OF SOCIABILITY

Flying squirrels are gregarious, living together in large groups at times. On two occasions I have observed seven in a single nest. One nest was located on the cross pieces of a pole supporting electrical lines close to a woods. The other was in a hollow beech stump. Three males were taken from a single large-toothed aspen on another occasion.

In captivity, as many as 40 flying squirrels were kept in a single cage thirty

inches square and five feet high. Even when given several boxes, the animals would congregate in one box during the warmer weather of the summer months as well as in the cold winter weather. During colder weather, however, the animals would bury themselves in the nesting material until one could not help but wonder how they were able to breathe.

LENGTH OF LIFE

Captive animals that were three years old exhibited such signs of old age as lack of activity, desire for sleep, and excess weight. Probably five years represents the normal life span of the flying squirrel.

CARE OF CAPTIVE FLYING SQUIRRELS

Flying squirrels proved to be readily adaptable to caged conditions. As many as forty-five animals were kept in cages at one time, and over one hundred were kept captive for varying lengths of time.

Two types of cages were used. The larger of these was constructed of a wooden frame, five feet high and thirty inches square. This frame was covered with one-half inch mesh hardware cloth. The top and bottom of the cage as well as all four sides were constructed of this material. The top of the cage was kept covered to protect the squirrels from rain during the warmer weather and snow during the winter months. Nest boxes of varying sizes were used, depending upon the number of squirrels on hand. A box six inches square with a round hole one and one-quarter inches in diameter in one side was large enough to accommodate ten squirrels. If larger nest boxes were used, one corner of the box was likely to be used for the deposit of excreta, making frequent cleaning necessary. This did not occur when the animals were kept in smaller boxes.

The smaller cages consisted of a roll of hardware cloth, eighteen inches in diameter with a plate of sheet iron wired to the top and bottom to close each end. The plate at the top was wired in such a manner that it might easily be removed. Such a cage was found to be satisfactory for breeding females. A small nest box, large enough for a female and a litter was wired to the side of such a cage. By gently tapping the nest box, the parent squirrel could be frightened from the nest and examination of the young was thus made possible.

The squirrels were fed in the evening before they became active. It was necessary during warm weather especially to place fresh milk or water in the cage in the morning as the squirrels often drank during the day. As was mentioned before, milk was used instead of water in order to insure a more adequate diet.

Activity wheels constructed of hardware cloth were freely used by the squirrels.

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THE INFLUENCE OF FLOOD AND LOW WATER LEVELS ON THE SURVIVAL OF MUSKRATS

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Investigations on the muskrat (*Ondatra zibethica zibethica*) in the Illinois River valley give irrefutable evidence to preliminary assumptions that fluctuating water levels are of prime importance in the welfare and management of this fur-bearing species. In a previous paper Bellrose and Brown (1941) reported a higher density of muskrat houses to a unit area in lakes with stable water levels than in the lakes with fluctuating water levels. Furthermore, stable and semistable water levels directly favored those species of plants that supported the highest population of muskrats.

The present paper covers the effects of floods and droughts on the survival of the muskrats in lakes along the Illinois River valley. Several investigators, particularly Errington (1937, 1939), have discussed some of the environmental vicissitudes muskrats face in nature. High productivity in the muskrat frequently results in overpopulation, which, with the advent of adverse conditions, causes intraspecific strife and mortality.

Muskrat habitats in the Illinois River valley may be placed in one of three general categories, namely, (1) habitats with stable water levels, (2) habitats with semistable water levels, and (3) habitats with fluctuating water levels. Characteristically, the lakes that lie on either side of the Illinois River are shallow and flat-basined, and with normal river stage have little or no current. These lakes vary in size from a few to 6,500 acres and aggregate at low stage about 56,000 acres of water surface.

Three of these lakes—Douglas, Rice and Chautauqua—are among the most productive of muskrat in the Illinois River valley. Douglas Lake is principally a river bulrush (*Scirpus fluviatilis*) marsh of some 1,300 acres with additional acreage of other plants and open water (Bellrose, 1941). Rice Lake, in 1940, had 413 acres of river bulrush and 317 acres of American lotus (*Nelumbo lutea*), as well as small beds of other aquatic plants. Lake Chautauqua has a periphery of 140 acres of marsh smartweed (*Polygonum muhlenbergii*) along with several hundred acres of black willow (*Sallix nigra*), about 45 acres of duck potato

(*Sagittaria latifolia*) and several acres of river bulrush. These lakes are characteristic of the stable and semistable water level group.

These lakes were the ones selected to determine the effect of floods on high and well-situated muskrat populations in 1941. Prior to 1939, Douglas Lake had semistable water levels. At the beginning of that year, however, the Peoria navigation dam was placed in operation, which raised and largely stabilized the water levels from that time to the arrival of floods, October 4, 1941. Rice Lake with semistable water levels generally has only small seasonal fluctua- 14 inches to 22 inches during the summer of 1941. The Lake Chautauqua National Wildlife Refuge, enclosed by levees, customarily has stable water levels (fig. 1).

Observations made during the latter part of August and the first of September, 1941, revealed an increase over 1940 in the number of muskrat lodges at Douglas

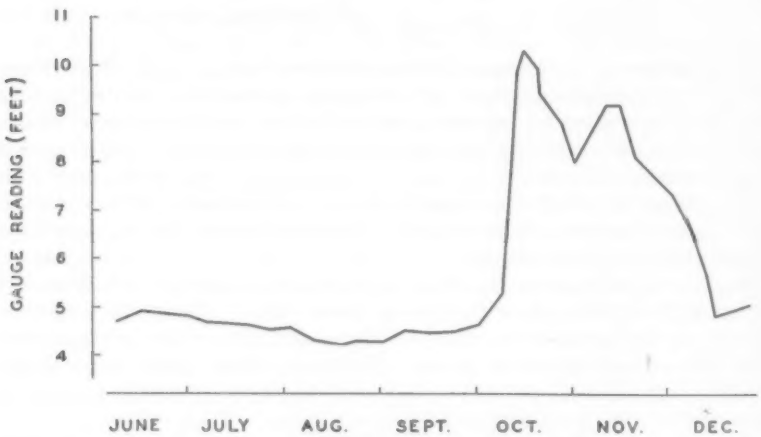

FIG. 1. Lake Chautauqua water level, 1941.

Lake. At Rice Lake there was a moderate increase in muskrat lodges, probably attributable to the 12-inch rise in water level in the river bulrush beds during the summer months of 1941. Lake Chautauqua contained in 1941 approximately the same number of lodges as it did the previous year.

REACTIONS OF MUSKRATS TO FLOOD WATERS

The seemingly favorable conditions that prevailed during the summer and fall of 1941 were suddenly altered by a sharp rise in the water levels, almost reaching flood proportions, in the Illinois River and adjacent fluviatile lakes by October 6. Figure 1 shows the profile of Lake Chautauqua for 1941. In a few days river water levels rose over lake levees and adjacent banks and thereby raised the water level in all bottomland lakes.

Douglas Lake.—A visit to the Douglas Lake area on October 9 revealed that

the water had risen seven feet and was still rising. Most of the river bulrush plants were completely covered by 18 to 24 inches of water, and adjacent dikes and lowlands were inundated. Where there had been at least 1,234 dwelling houses (based on previous year's count), there was scarcely a house left. Most of the houses had risen with the water, becoming in a short time mere floating piles of vegetation. A strong wind and accompanying wave action knocked many of them apart and blew others in among the partly submerged willows and buttonbush (*Cephalanthus occidentalis*). These plants occurred in small scattered clumps over the area and in a thin strip along a small levee that separated the upper two-thirds of the lake from the lower part. Other muskrat houses had been swept in among the willows and protruding tops of river bulrush

TABLE 1.—*Number of muskrats on refuge sites in three sections of Douglas Lake, October 9, 15 and 19, 1941*

DATE AND PLACE	REMNANTS OF LODGES			RAFTS OF DEBRIS			TREES OR LOGS			AVERAGE NO. OF MUSKRATS PER REFUGE SITE
	No. of sites	No. of muskrats	Ave. no. per site	No. of sites	No. of muskrats	Ave. no. per site	No. of sites	No. of muskrats	Ave. no. per site	
October 9, 1941										
Open lake	22	114	5.2	69	364	5.3	19	73	3.8	5.0
Levee	50	218	4.3	48	109	2.3	16	29	1.8	3.1
Periphery of lake	79	58	0.7	37	109	3.0	7	16	2.3	1.5
Totals	151	390	2.6	154	582	3.8	42	118	2.8	3.1
October 15, 1941										
Open lake	8	48	6.0	27	148	5.5	1	3	3.0	5.5
Levee	51	191	3.7	10	27	2.7	11	18	1.6	3.3
Totals	59	239	4.0	37	175	4.7	12	21	1.7	4.0
October 19, 1941										
Levee	51	48	0.9	—	—	—	6	6	1.0	1.0

on the east side of the lake. In the latter location there were in addition to the wave-swept debris a few houses still anchored and serviceable.

Everywhere on the lake the muskrats were in dire and critical straits. At best, there was little protective cover for the remnants of the lodges and their inhabitants. Both the dwellers and the dwellings were being buffeted by heavy waves. The scenes of struggle for life against the elements were most vividly enacted, particularly where the remaining houses were floating rafts of debris caught in the tops of buttonbushes.

While it was impossible accurately to ascertain animals on every place of refuge, it was possible to secure fairly accurate samples. The muskrats apparently were so preoccupied in their plight or so exhausted that they allowed us to pass within a few feet before plunging from their resting places.

Table 1 reveals the number of refuge sites, the total number of muskrats and

the average number on a refuge site for several distinct zones in Douglas Lake. Since most of the lodges were formerly located in the center of the area, it is not surprising that 551 muskrats, the largest number enumerated, were attempting to maintain themselves on the then open water. The majority were on rafts of debris, which, for the most part, had drifted until caught in the protruding tops of buttonbushes. In this exposed situation there were 5.3 muskrats per raft, while there were 5.2 animals on floating houses in similar straits. Not only do these high densities show the lack of sufficient refuge sites, but the fact that 73 muskrats were forced to seek sanctuary in the branches of buttonbushes indicated that in this section they were in critical need of refuges. Furthermore, waves were tearing asunder many rafts, the occupants of which were making valiant but often futile attempts to keep from being washed into the water.

On one occasion an adult, presumably a female, picked up a kit from a rapidly disintegrating debris pile, held it above the water, and swam 25 yards to a more substantial mass of vegetation. There the kit was deposited beside two others, evidently previously rescued in similar fashion. Two large muskrats had somehow managed to secure a resting place four feet above the water on the top of a leaning post. In the few large willows as many as seven to eight muskrats were observed stacked in crotches, one on top of another. Before the bottom individuals could leave, as we cruised by, barely feet away, the top ones had to dive. On several occasions individuals were noted as high as three feet above the water. Numerous muskrats were seen swimming, some aimlessly, others toward a place of refuge. Kits were frequently noticed that were blindly, desperately trying to mount floating fragments of vegetation.

A sample count along one mile of the willow-covered inundated levee, which divided Douglas Lake into two areas, showed 115 houses and rafts lodged in the willows. Prior to the high water, only a few houses were along the levee; however, following the advent of high water and wind many floating houses came to rest there. According to data presented in Table 1, this section furnished much more protection from the elements than the buttonbush clumps in the open lake. Crowding was noticeably less; there were 31 percent fewer muskrats per refuge site. Further evidence that this population was more secure than those in the previous habitat is evident from the much higher proportion of animals on lodges than on rafts or in trees.

Around the periphery of the lake, where the water was noticeably shallower, 123 muskrats were enumerated. Of the 86 lodges recorded, 41 contained no muskrats. The remaining lodges averaged 1.4 muskrats per dwelling. We believe that so few muskrats were observed on the outside of these lodges because they were able to remain inside in the dry chambers. That the muskrats were still in these lodges was evident since on several occasions we saw one or two muskrats appear at the edges of houses, climb up on the outside and commence to feed. In deeper and more exposed parts of this peripheral zone, houses had been dismantled, although not to the extent that they were elsewhere. Data in Table 1 reflect this, showing 3.0 animals per raft of debris and 2.3 per occupied willow. Since the average refuge site harbored only 1.5 exposed muskrats, this

zone must be regarded as the safest and the one having the most secure population.

On October 15, six days after making the first observations on Douglas Lake, we returned to find the water levels were still high. Enumeration of refuge sites and their inhabitants showed that in the open water a number of rafts and remnants of lodges had further disintegrated. That some survivors from these sites secured refuge elsewhere is evident from data presented in Table 1. There were 0.8 more animals to a lodge and 0.2 more to a raft in the open water than there were on the previous occasion. If the mortality of many of the resident kits and other age groups was deductible, the data would show that even larger numbers had moved to the available sites. Since the largest increase occurred on remnants of lodges, it is evident that animals were sufficiently strong to search for the safest sites available. A decrease of 0.8 animals to an occupied willow may be attributable to movement or to mortality of the muskrats in these vulnerable positions.

Further observations, on October 15, showed an increase of 0.2 muskrats to a refuge site along the levee. Also, a slight increase in the number of muskrats in trees, an increase in the number to a raft of debris and a decrease in the number to a remnant of lodge were recorded. Of interest is the increase of muskrats on the rafts of debris along the levee, while at the same time a decrease occurred in the number to a lodge. Rafts of vegetation as well as lodges had been enlarged considerably, enabling each to support more animals. The muskrats on the rafts, however, were still exposed to view, whereas those in the make-shift lodges were often hidden from view and possibly overlooked. Increased number of animals to a refuge site is indicative of ingress from the open lake.

By October 19, ten days after we made the first observations, the water in Douglas Lake had dropped about 20 inches from the crest. Observations made along the inundated, flooded willow levee showed that the muskrats were fast becoming well situated (Table 1). Only 48 muskrats, 0.9 to a lodge, were exposed to environmental vicissitudes. None was found on rafts of debris and only six were seen in trees or logs. Close scrutiny revealed that few muskrats were on houses and rafts because they were well concealed in alcoves and chambers in the structures.

In the case of the majority of the rafts and partial lodges among the branches of the willows, the muskrats had continued to build onto the lower parts of the structures as the water receded, resulting in new structures below the old and forming two-story edifices partly open at the sides. These structures afforded comparatively safe and protected retreats to the muskrat population of that area, thereby greatly reducing vulnerability to predation and to the elements.

Rice Lake.—Flood water did not commence to rise in Rice Lake until October 9. Water flooded the chambers of muskrat houses situated over most of the lake on October 10, but the lodges were then still anchored and substantial. Flooding of the chambers, however, did force the inhabitants to seek refuge on top of the houses. Many lodges held from four to seven individuals in cup-shaped depressions in the domes. By October 11 the water level had risen 6.5

feet, which dislodged houses from their foundations. A moderate south wind blew the floating houses into the buttonbush and willows bordering the northwest section of the marsh. In a matter of a few hours many of the lodges were completely demolished by waves. Debris from wrecked lodges formed a mat of vegetation one-half mile long and from 2 to 10 yards wide.

Relatively few individuals were exposed on any of the refuge sites on Rice Lake (Table 2). An average of only 1.1 muskrats was observed to a remnant of lodge or raft of debris. Of 30 individuals seen 49 percent were kits, a much higher ratio than at other lakes. The small number of animals observed, the low number to a refuge site, and the comparatively high number of kits, were apparently attributable to the abundance of cover. Hundreds of acres of flooded, dense bottomland timber lay behind the line of wrecked muskrat lodges. Observations made showed that the large, strong adults and juveniles left the exposed sites for the shelter of the flooded woods. On pushing a boat through the brush we could hear numerous splashes denoting muskrats diving from floating logs, piled debris and other refuge sites. Thus, because of flooded,

TABLE 2.—*Comparative numbers of muskrats on various places of refuge on Lake Chautauqua, Rice Lake and Douglas Lake*

LAKE	REMNANTS OF LODGES			RAFTS OF DEBRIS			TREES OR LOGS			AVERAGE NO. OF MUSKRATS PER REFUGE SITE
	No. of sites	No. of muskrats	Ave. no. per site	No. of sites	No. of muskrats	Ave. no. per site	No. of sites	No. of muskrats	Ave. no. per site	
Douglas Lake.....	151	490	3.2	154	582	3.8	42	118	2.8	3.4
Rice Lake.....	10	11	1.1	17	19	1.1	—	—	—	1.1
Lake Chautauqua.....	24	64	2.7	5	11	2.2	6	6	1.0	2.3
Totals and Averages..	185	565	3.1	176	612	3.5	48	124	2.6	3.2

dense woody vegetation surrounding Rice Lake, muskrats were afforded much better refuge than at Douglas Lake. Since the population was less vulnerable, survival must certainly have been greater. Trapping records showed an actual increase of muskrats caught in 1941 over 1940, which substantiated this premise.

Lake Chautauqua.—Water levels on Lake Chautauqua commenced to rise the first week in October (fig. 1). By the middle of that month the water had risen 5.5 feet, reaching the peak. On October 13 we visited certain sections of the lake. Where some 50 houses had been situated in a duck potato bed, not one was visible; all had either floated away or become inundated.

In an adjacent grove of black willow trees, through and around which marsh smartweed beds occurred, only a few sodden lodges remained of the 80 formerly situated there. Many of the muskrats were resting on willow-twig platforms built in crotches of the black willows at the water line. At the south end of the willow grove, floating duck potato stems had been added to the platforms, and on the periphery were several rafts composed of duck potato stems. Data gathered in this area (Table 2) revealed that there were 2.7 muskrats to a house or platform; 2.2 to a raft and 1.0 to an occupied tree or log. By comparing the

numbers on these refuge sites with those on similar refuge sites at Douglas Lake and Rice Lake, it is evident that Chautauqua muskrats were more secure than those at Douglas Lake but less secure than those at Rice Lake.

That a larger number of muskrats occurred to a lodge at Douglas Lake than at Lake Chautauqua was an indication that muskrats at the former place were forced by greater destruction of lodges to concentrate (in larger numbers) on the remaining lodges. Waves breaking apart Douglas Lake rafts accounted for a high of 3.8 animals to a raft, while at Lake Chautauqua, where greater protection from the elements was afforded, only 2.2 muskrats were forced to remain on such sites. At Rice Lake only 1.1 muskrats elected or were forced to remain on such sites, and none found it necessary to seek sanctuary in tree branches. Whereas 3.8 individuals occurred to an occupied tree in Douglas Lake, only one was found to an occupied tree site at Lake Chautauqua.

Thus, where possible, muskrats sought to remain on the tops of lodges; next they preferred floating rafts of vegetation debris, and, lastly, branches of willows and buttonbush. Crowding was severest where wooded shelter was lacking.

TABLE 3.—*Comparative numbers of kits and old muskrats per refuge site at Douglas Lake, 1941*

PLACE	DATE	NUMBER OF ANIMALS PER REFUGE SITE	
		Kits	Other age groups
Open lake	October 9	2.2	5.3
	October 15	1.4	5.3
Levee	October 9	1.5	3.1
	October 15	1.4	3.2

As discussed under intraspecific strife, fighting was most severe where crowding and exposure occurred and least where individuals were scattered and shelter was best.

LODGE AND RAFT CONSTRUCTION

We are interested in ascertaining the effect high water, arriving as it did after the completion of most houses and the withering of marsh vegetation, would have on fall and winter quarters of muskrats.

Despite the lack of suitable material and the severe environmental conditions, muskrats were attempting to build some lodges higher, repair others, and, of necessity, build rafts. At Douglas Lake, October 9, at least 14 individuals were noted carrying material to rafts, platforms, and demolished lodges, often from as far as 15 to 30 yards, unusual distances for them to seek building material in this vicinity. Fortunately, masses of duck potato stems had floated to the surface and muskrats made extensive use of them. Practically every lodge and raft was being built around the branches and limbs of willows or buttonbushes, but logs, floating boards, boats, and duck blind platforms were also being used as lodge foundations.

By October 19, Douglas Lake had receded 20 inches and newly built muskrat

lodges were beginning to assume large dimensions. Most of them were no longer open at the sides and concave at the top, but contained interior chambers, entrances to which were either above or below the water surface. Many platforms built in tree branches 10 days earlier had been left high and dry.

As the water receded still further, muskrats continued to add to the bottoms of the house, until some structures assumed gigantic and unusual shapes. This was especially noticeable at Lake Chautauqua where structures were often cradled for six feet or more in willow trees. The sharp drop in water levels during the first part of December left many houses suspended in the air, the base some 18 to 24 inches above the water surface (Pl. 1). After the houses and debris piles on logs and boats had been suspended by the recession of the water, muskrats at Rice Lake moved out to the river bulrush beds bordering the bottomland lakes. There, in early December, they constructed their third set of houses, using stems and leaves of river bulrush.

When Douglas Lake houses were exposed along the willow-covered levee, muskrats dug tunnels from the lodges through the crown of the levee to the water. With the return of a normal water level, only a few muskrats moved from the levee and periphery of the lake back to the center of the marsh.

Muskrats used a wide variety of materials to construct refuge rafts and lodges. At first, much of this material consisted of floating vegetation debris. At Douglas Lake, duck potato and river bulrush stems were widely used. Rice Lake muskrats used soft maple leaves, giant ragweed stems, available grasses, and woody vegetation. Muskrats on Lake Chautauqua used willow twigs and floating duck potato stems to construct refuge platforms in the forks of willows. As the supply of floating debris became exhausted and the crisis caused by high water subsided, the muskrats sought submerged river bulrush and marsh smartweed with which to build new lodges.

ACTIVITY AND FEEDING

During the first few days of exodus from their flooded dwellings, muskrats were, for the most part, lethargic. Those that were active either were feeding or constructing refuge places. It was easy to pass within a few feet of the resting animals without disturbing them. This was true especially in the inundated marsh area of Douglas Lake, where the greatest battle for existence was fought. At Rice Lake, because of the protection offered by brush and logs, adults and juveniles were quite active, but kits were noticeably torpid. Elsewhere adults were the first to depart from refuge sites, followed by juveniles, with kits consistently the last to leave. In general, the sluggish attempts of the muskrats to elude danger bespoke the physical battering that they had undergone.

Emergency rations were the order of the day, but muskrats were equal to the emergency. At Douglas Lake, where river bulrush, pickerelweed (*Pontederia cordata*) and marsh smartweed had been the staple items of diet, the muskrats changed to twigs and bark of buttonbush and willow, coontail (*Ceratophyllum demersum*), duckweeds (*Lemna*, spp.), river bulrush, and duck potato. River bulrush tubers obtained from lodges and succulent duck potato stems were

PLATE 1

As the flood water receded the muskrats continued to add to the bottoms of the houses until some structures assumed large and unusual shapes.

PLATE 2

Black willow bark formed an important part of the emergency diet of the muskrats during the flood.

floating abundantly on the water. Individuals were noted climbing among the branches of buttonbush and willows to feed on the twigs and bark of these species.

Muskrats at Rice Lake were more fortunate. There, demolished lodges of river bulrush, American lotus, and pickerelweed adjacent to timber shelter furnished a ready food supply. Adults and large juveniles were noted leaving the flooded thickets to forage on bulrush tubers and lotus heads. Kits fed extensively on duckweed, as they also did at Douglas Lake. Later, muskrats were observed diving in eight feet of water to obtain pickerelweed stems and river bulrush tubers.

Normally, Lake Chautauqua muskrats depend principally on marsh smartweed rootstocks for subsistence. However, with rootstocks too difficult to obtain, they resorted to black willow bark (Pl. 2), completely denuding the upper side of many willow trunks and branches. Here again, individuals were noted feeding also upon duckweed and duck potato.

INTRASPECIFIC STRIFE

With the shifting of muskrats from home territories and with the ensuing crowding of adults, juveniles, and kits, much intraspecific strife was noted, particularly among the least secure individuals. Douglas Lake (October 9) was the scene of several battles. In the open lake two adult muskrats were observed fighting over the possession of a partly sunken lodge. One, the attacker, made repeated sallies at the other, finally succeeding in driving it away. An adult was seen violently attacking five kits on an almost completely submerged lodge. While one kit was desperately trying to regain its place of refuge, the assailant slashed the fore part of its head off. On other refuge sites, two dead kits were picked up, one with its body cavity cut open, the other with its hindquarters slashed. Again, one kit was found with its rear legs badly mangled, and a kit was discovered, still living, with its intestines protruding from an open wound. Six days later, two dead adults were picked up at Douglas Lake; a punctured body cavity in one individual and a slashed shoulder in the other were visible signs of strife.

Along the levee at Douglas Lake, muskrats were more secure than in the open water area, and consequently little strife was noted. Only one individual was seen that bore evidence of fighting; it had been bitten through the nose.

Because of the extensive flooded timber at Rice Lake and the protection it afforded refugee muskrats, there were very few concentrations of animals or instances of marked strife. On one occasion a juvenile came too close to a feeding adult, and was immediately chased. The pursued juvenile unsuspectingly dashed toward a feeding kit, which immediately beat a hasty retreat.

Intraspecific strife at Lake Chautauqua appeared to be higher than at Rice Lake and lower than at Douglas Lake. This would be in keeping with the relative security of the various populations. Evidence was seen that several Lake Chautauqua muskrats had been fighting. One large juvenile with its tail badly chewed was so weakened that it could barely navigate.

MORTALITY

As alluded to above, intraspecific strife often resulted in mortality. In addition, a half dozen large and medium individuals and four kits were picked up that showed no external injuries. Hunters and trappers reported finding numerous muskrat carcasses that had no discernible marks of violence. Disease and drowning had presumably caused their deaths.

Limited observations prevented ascertaining the exact loss of life caused by the elements and predation, but populations, exposed as they were, suffered. Kits, in particular, were chilled, torpid, and less capable of seeking safe sites than were larger individuals. Loss in the kit group was undoubtedly greater than among adults or juveniles. Table 3 shows the relative loss between kits and older individuals for two areas of Douglas Lake. As expected, kit loss was greatest in the open water area, where the muskrat population was most vulnerable to drowning and predation. In the open lake during a six-day period the number of kits per refuge site dropped 0.8, whereas the number of individuals to a refuge site in other age groups was not reduced. Kits were reduced 0.1 to a levee refuge site in the six-day period, while other age groups increased 0.1 to a refuge site, evidently the result of ingress from open water areas. Because of the continued destruction and construction of lodges and beds it was impossible to measure the actual loss among adults as was done with the kits, but it appears to be lower than one would suspect.

Predation, practically impossible to evaluate, must have been severe. Mink (*Mustela vison*), marsh hawk (*Circus hudsonius*) and barred owl (*Strix varia*) were abundant in all the areas, and the exposed muskrats certainly were easy prey. At Rice Lake, where the muskrat population was least vulnerable, a marsh hawk was observed to make repeated sallies on those animals.

Since muskrat houses are, in general, indexes of the muskrat population on areas where few bank dens occur, house counts made on Lake Chautauqua in 1940 and after the high water in 1941 gave a picture of a reduced population attributable to the flood. In January 1941, 636 dwellings were enumerated as against 242 in January 1942, after the fall flood of 1941. Trappers caught 2,137 muskrats on Lake Chautauqua during the 1940–41 season, and but 1,263 during the 1941–42 season. The catch during the latter period would have been somewhat higher had not unfavorable weather shortened the season. Concensus of the trappers was that the bulk of the muskrats had been taken; this was substantiated by succeedingly lighter catches during the last week of trapping.

INFLUENCE OF RECEDING WATER LEVELS ON MUSKRATS

In recent years, water levels below normal have actually been more prevalent than water levels above normal in the Illinois River valley. In addition to natural influences causing water levels below normal, many duck clubs lower the water levels of their lakes to expose all or part of the lake bed during most of the year, raising the water level only during the hunting season. Observations made on such areas, during the past three years, reveal that such a practice is

detrimental to resident muskrats, and that the recession of water has at least as great an effect on muskrat populations as does abnormally high water in the Illinois River valley.

There were 279 muskrat houses on 419 acres of marsh at Cuba Island in February 1940. New houses had been constructed and old ones repaired during August and September, 1939, after a favorable summer during which water levels of the marsh fluctuated from 12 to 30 inches. The water was lowered the last of December so that the bases of 175 houses were exposed. There were no tracks, cuttings, feces or other muskrat signs about the exposed lodges. Around the other lodges, in shallow water, there was much evidence that they were inhabited. It is conjectural how much of this loss was represented by egress to ditches and other bodies of water and how much was due to predation. There was no evidence of predation slightly over a month after the water was lowered.

Water levels lowered during the summer of 1940 to expose the basins of South and Horn lakes resulted in an exodus of most of the 200 or more muskrats residing there. In August 1940, less than 15 individuals were attempting to live in those areas. They were inhabiting tunnels, filled with water, that ran below the lake bed from their quarters to feeding places on the dry basin. The quarters were above the water table, in a slight bank, among the roots of buttonbushes.

Normal water levels were restored to South and Horn lakes the first of October 1940. Trapping after December 15 of that year yielded 93 adults and large juveniles and no kits from South Lake and 30 large and medium individuals and 2 kits from Horn Lake. Thus, kits formed only 1.5 percent of the trapped population in that area, but formed 10 percent of the trapped population in other lakes in the river valley. The logical assumptions, based on the above data, are: (1) An influx of adult and large young of the year took place in the above lakes from surrounding areas a short time after the habitat was made more favorable by the return of a normal water stage. (2) Despite the population being low, fewer young were born there in October, as was evident from the low number of trapped kits, than in adjacent areas which had remained more favorable throughout the year.

In 1941, the water levels were again lowered during the summer at South and Horn lakes and again a bare dozen individuals attempted to summer in subterranean burrows. Water levels were raised to above normal in these lakes by floods early in October. Trapping after December 15, 1941, yielded only 9 large muskrats at South Lake and 15 large ones at Horn Lake. The repopulation of these areas by outside individuals was, therefore, considerably less in 1941 than in 1940. The dearth of muskrats in 1941 may at least in part be conceivably attributed to a reduced population in the entire area by flood waters as recounted earlier.

A survey of Clear Lake in September 1940, when over 50 percent of the Lake basin was exposed, showed approximately 40 muskrats present. They were concentrated in bank burrows and in dry-situated lodges along spring runs. The houses were undermined by burrows which led to water and feed sites. Many muskrat trails led above ground from the burrow entrances to river bul-

rush and duck potato beds. The water level was raised in early October to a level still subnormal. Nevertheless, there was an influx of muskrats, presumably from adjacent Lake Chautauqua, since over 125 animals were trapped. One trapper caught 55 large specimens, where less than 10 individuals occurred two months previously.

In 1938, Rice Lake muskrats were situated in river bulrush beds. Water levels fell 18 inches in 1939, with the result that, for the most part, the residents built their lodges in the American lotus zone. In certain sections, however, muskrats attempted to remain in their original home territories despite little or no water. During the summer, one group existed in subterranean chambers, the tunnel entrances of which were found on the exposed lake bottom, among the vegetation. From the entrance the tunnels ran to a small bank where enlarged chambers were above the water table. Well beaten runs were visible through the vegetation from the tunnel entrances to feeding sites. Other muskrats remained and built lodges in water a few inches deep, digging deep canals from the lodge entrances to feed sites.

Animals in these two situations remained in apparent security until winter. With subzero weather in January, water in subterranean tunnels froze, forcing the subterranean inhabitants to create external openings to their bank nest chambers and to wander in search of food. Even though the shallow water froze to the bottom at that time, muskrats living in houses built in shallow water were able to reach food by digging new canals below the ice to river bulrush rootstocks. When the frost line penetrated the lake bottom, however, these muskrats were forced to gnaw through the lodges and to wander about on the ice searching for food. As might be expected, animals exposed on the ice were subject to predation. Approximately 20 muskrat carcasses were found by Charles Cooper, local resident at Rice Lake. All displayed the characteristic marks left by mink in killing their victims.

Too little water, like too much water, resulted in the muskrats attempting to relocate themselves in more favorable habitats. This movement sometimes was within the area but more often was to adjacent areas. Fortunately, such forced exoduses occurred at a time when the muskrat habitats were in general underpopulated. A part (usually a very small percentage) of the muskrat population, however, invariably attempted to summer or winter in their home territories, despite the paucity of water.

DISCUSSION

There can be little doubt that a rise of five to seven feet of water during flood stage disrupted and reduced muskrat populations in certain areas of the Illinois River valley in October 1941. Exceptionally favorable environmental conditions, prior to high water early in October, had resulted in higher, better situated populations than usual.

Muskrats were not without adaptability to meet the crises of flood water. They attempted to repair and build their lodges higher and when the chambers became flooded they sought refuge on the tops. Continued rising water and

wind demolished many lodges, forcing the inhabitants to seek refuge on rafts of debris and in willows and buttonbushes. The largest number of exposed and, therefore, most vulnerable individuals occurred at Douglas Lake, followed by Lake Chautauqua and Rice Lake. The differential security afforded these animals in the various habitats was related to the distance from, and the quantity and cover density of, flooded woody vegetation.

The greatest intraspecific strife occurred among the most exposed muskrats, as illustrated by the amount of fighting seen in the open water area of Douglas Lake. There the number of refuge sites continued to be reduced, forcing more and more animals to crowd together on inadequate sites. With a high of 15 individuals recorded on one site, it is little wonder that the struggle for existence was great. Numerous muskrat carcasses were found, which, when autopsied, showed that death was caused by muskrat-inflicted wounds, and possibly drowning, disease or exposure. Predation was difficult to evaluate, but since mink and barred owls were common in the region and the animals were lethargic and exposed, it was doubtless great.

Cognizance has been taken of the effect high water may have on fairly high muskrat populations. While such occurrences are the exception rather than the rule, it is also true that the effect may be extensive, thereby perhaps seriously depleting the muskrat population over a wide area. Depletion from such unnatural climatic causes may thus necessitate reduced muskrat trapping to insure against further depletion in the marshes.

The use by muskrats in flood times of anything substantial enough to support themselves suggests that as a temporary management measure the provision of logs or board rafts, anchored to the bottom of the lake, might be of service. Such a measure would reduce crowding and lessen the danger of drowning and intraspecific strife.

While muskrats may be harassed and decimated within a short time during flood conditions, those living under low water conditions may escape without serious loss in summer but may be seriously affected during cold, winter weather. Particularly is loss likely to be great when the muskrats are forced to leave their quarters in search of food. Whether muskrats dwelling under drought conditions in summer succeed in raising many young is problematical. Ratios between kits and animals of other age groups, caught in trapping, reveal many more young are born during the fall in areas not subject to low water during the summer than in the areas that are. This tendency appears to be maintained even when normal water levels are restored to the low water areas early in the fall; these areas still remain underpopulated despite an ingress of animals from other areas. That there is often a fall influx of muskrats to low water areas, after a rise in the water levels, can be little doubted.

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NOTES ON THE SAGE MOUSE IN EASTERN OREGON

BY A. W. MOORE

This mouse has been recorded in the literature under various names: pigmy vole (Bailey 1900), the sage-brush meadow mouse (Anthony 1913), the pigmy meadow mouse (Anthony 1928), the pigmy mouse (Bailey 1936) and a possible subspecies of the sage-brush meadow mouse (Hall 1928). As there are mice of other species with smaller bodies, the writer is dropping the diminutive qualification and, the mice studied having been found in sage-brush range, the term pertaining to grassy or sod land is omitted.

Collected specimens were said by H. H. T. Jackson (*in litt.*) to be referable to *Lemmiscus pauperrimus*. Goldman (1941) states "The animal now recognized as *Lemmiscus pauperrimus* is evidently very closely allied to *L. curtatus*, . . ." and presents the subspecific name, *L. curtatus pauperrimus* (Cooper). This status followed Anthony's (1928) presentation of the sub-genus *Lemmiscus* under the Old World genus *Lagurus* after which Davis (1939) raised the form to full generic rank.

The location of the area from which the data were obtained is about 36 miles west of Burns, Oregon, in the arid transition zone at an elevation of approximately 5,000 feet. Big sage (*Artemisia tridentata*) and black sage (*A. nova*) form the predominant cover. Rodent-range relationship studies had been conducted at the Squaw Butte Range Experiment Station and in the vicinity at intervals since the fall of 1939.

Prior to trapping done in 1941, but one sage mouse was taken in approximately 3,500 trap nights that had yielded conservatively 1,200 small rodents. However, about the middle of May, 1941, a heavy population of sage mice was noted in a number of locations on the stock ranges being studied and indications were that the population was rather common over an area embracing some 36 townships. Mr. L. K. Couch reported their presence in early August, 1941, in abnormal numbers on the Hart Mountain Antelope Refuge located about 100 miles south of the study area and stated that his attention had been attracted to them by the presence of large numbers of short-eared owls (*Asio flammeus*). Much of the Hart Mountains is in the Canadian zone.

One of the heavily populated areas, a 6 acre plot located in what is termed Range 3, had been subjected to two brief composition inventory trappings in October and November, 1940, when 96 trap-nights yielded no sage mice. The first trapping on this area in 1941 yielded, for the 24 hour period from the evening

of June 9 to the evening of June 10, 18 sage mice and 13 other small rodents from 36 traps. Fifteen of these sage mice were females.

Normally the number of males and females of mammalian species is reported to be approximately equal. The accompanying table shows that at what was apparently the peak of population there were more than three females to each male and that as the density appeared to wane, the ratio tended to reverse. The sex ratio of the population as it was building up may only be conjectured. Trapped males were examined for possible sexual mutilation and none was found to be incapacitated. Examination of four sets of sage mouse embryos by Jacob Frenkel of the University of California showed two sets to contain four males and two females, one set to contain one male and six females and one set with no males and six females.

Other rodents taken as represented in the table consisted mainly of *Perognathus* and *Peromyscus*. Sex ratios for these were normal. The take from the plot in

TABLE 1.—*Trapping records from 2 plots of 6 acres each (Squaw Butte Range Experiment Station) Burns, Oregon*

	TRAP-TAKE PERCENTAGE[1]			ACTUAL NUMBER TRAPPED OF ALL GENERA
	All genera	♂ Sage mice	♀ Sage mice	
Range 3				
June 10–17[2]	59	8	27	207
June 23–25	37	6	14	169
July 28–31	51	4	2	271
Range 7				
June 26–28	46	4.5	3.5	209

[1] Percentage of mice caught in each 100 traps.

[2] Hail storms reduced severely catches on June 17, July 28 and 31 by springing traps.

Range 7 shows a reversal in the sex ratio for a comparative period to that in Range 3 and a hazarded explanation would be that the habitat was less favorable as evidenced by less rugged sage-brush. Figures in the table do show that where the sage mice predominate in numbers the female of the species outnumbers the male.

These mice appear to breed throughout the entire year. On October 28, 1941, a female showed four distinct uterine scars and on December 7 the same year a very fat breeding male was taken. The smallest pregnant animal taken had a total length of 114 mm and yielded seven uterine sacs having a diameter of 2 mm. The largest sage mouse taken, a female, measured 141–29–16 mm. Size of litter ranged from 4 to 10 as shown by embryos or uterine scars that were unquestionably distinct. June breeding records show the following: 3 with 4, 18 with 5, 20 with 6, 21 with 7, 3 with 8, and 1 with 10. That the minimum number was 4 instead of a lesser figure for a series of 66 females shows a relatively high breeding potential.

The living quarters of these animals were normally found under sage-brush that was dead or of low vitality. As for the most part they had taken over systems of other rodents, the condition of the sage was not attributed to the current habitants. Stone retaining walls, rubble piles and road borders thrown up in loosely piled ridges also served to provide living quarters.

Runways were distinct and located under and between brush clumps on the study plot. Full advantage was taken of existing cover. Trail building habits were noted by Hall (1928) in Nevada, but Bailey (1936) minimizes this habit due, probably, to not having found populations of sufficient density.

Activity was on a full time basis, although on bright days travel appeared to be motivated primarily by a desire to go to or return from a certain shelter in the least possible time. On cloudy days the rate of movement was less rapid and individuals were seen as they were feeding. Records show that but 36 of the 247 trapped from the plot in Range 3 were taken between the hours of 4:30 a.m. and 5:00 p.m. As many of the traps were set on mouse trails it is indicated that the daytime catch was the result of travel and not due to feeding.

Work was discontinued on the area the last of June and not resumed until late July. In the interim the heavy population of sage mice had experienced a severe die-off. The lethal cause is unknown although it is known that from July 13 to 17 exceptionally high air temperatures were recorded. The accompanying table indicates that the numbers of other species were not reduced. No indication of migration was present nor did the more sheltered sites show populations that were not decimated.

During the late July period, approximately fifty sage mouse quarters were dug out, revealing dead in all stages of decomposition. No living new born young were found. Nest cavities had in every known instance at least two entrances. Size of the nest pocket was approximately four inches in diameter and depth under ground varied from just below the surface to approximately 10 inches. Length of runways varied greatly as in several places pocket gopher (*Thomomys talpoides quadratus*) runways had been appropriated. Nest material consisted, for the greater part, of shredded blades of dead grass. Several of the nests had coarse sage-brush bark for the outer layer. Aside from a few sage-brush leaves, no food was found in the nest or runways at this time.

The food of these mice was varied. During June, Sandberg's bluegrass (*Poa secunda*) and Collinsia (*Collinsia parviflora*) were taken, probably because they were plants growing under sage-brush cover. Indications later were that the other grasses were taken when their seed was in the soft dough stage. Consumption was under protective cover, and seed tops and stem nodes appeared to be preferred. Very little edible material was taken into their burrows. During July, heavy pressure was applied to squirreltail bunch grass (*Sitanion hystrix*). This grass has diffuse basal blades that provide excellent cover. Underneath these twisted lower leaves the mice proceeded to eat into the succulent crown. Culms and leaves were mowed off. Aside from the few sage-brush leaves found during the burrow excavations in July, no indications of feeding on sage-brush were seen. Hall's (*op. cit.*) reference to the denudation of sage-brush was con-

nected with under snow activity. No such habits were noticed on the writer's study area which would imply that there was not sufficient snow cover or that sage mice were insignificant in number. Severe defoliation of sage-brush observed on the area, however, was due to the activity of ants.

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RODENT POPULATIONS IN THE SAGEBRUSH DESERT OF THE YAKIMA VALLEY, WASHINGTON

BY JOHN A. GRAY, JR.

During the summer of 1941, a party from the George Williams Hooper Foundation for Medical Research was led by Dr. William McD. Hammon to the Yakima Valley, Washington, to determine the reservoirs and vectors of the Western Equine and St. Louis strains of encephalomyelitis epidemic there. An attempt was made by me to determine the population of certain rodents in the sagebrush desert and to investigate the merits of a variation of the Sherman live trap obtained from Mr. Everett E. Horn of the Fish and Wildlife Service. If these live traps are valid instruments for rodent censuses, many problems can be solved without trapping out desirable study areas.

In order to test the live traps two methods were employed: a quadrat containing 100 Victor mouse snap-traps was set near a quadrat containing 100 live traps, and the results compared. Two such pairs were run. Then a single quadrat of the same dimensions, containing 100 of each type of trap was set, and separate records were kept for the two types of trap. All live-trapped animals were removed from all quadrats when caught. Traps were cleared and rebaited morning and evening.

The quadrat method used was that of Bole (1939), in which a square 150 feet on a side is laid out and enough traps placed in it to catch all the rodents there

in three nights. The total catch for three nights in a single quadrat, multiplied by two, is taken to represent the rodent population of an acre of this type of habitat. Bait in all traps was rolled oats of the type used for livestock feed. This was placed on the pan of the snap traps and on the treadle inside the live traps.

Paired quadrats were never set closer to each other than 300 yards nor farther apart than 500 yards. Sites as nearly alike as possible were selected for paired quadrats, but the three series were set in different types of terrain to provide a cross section of the sagebrush desert of the valley. Quadrats 1a–1b were on a flat $1\frac{3}{4}$ miles northeast of Moxee; 2a-2b were in a north-facing, rocky ravine on Ahtanum Ridge, south of Yakima; 3 was on a flat in Terrace Heights, east of

TABLE 1.—*Results of comparative trapping on five quadrats in eastern Washington*

SPECIES	1a (SNAP)	1b (LIVE)	2a (SNAP)	2b (LIVE)	3 (SNAP)	3 (LIVE)
Eutamias minimus	1	0	2	3	0	0
Perognathus parvus	22	23	2	3	17	14
Onychomys leucogaster	0	0	1	0	0	0
Reithrodontomys megalotis	3	3	0	0	5	1
Peromyscus maniculatus	2	0	2	6	0	0
Total	28	26	7	12	22	15

TABLE 2.—*Estimated population of active rodents per acre*

SPECIES	NUMBER OF INDIVIDUALS	PER CENT OF TOTAL FAUNA
Eutamias minimus	2.4	5.5
Perognathus parvus	32.4	73.6
Onychomys leucogaster	0.4	0.9
Reithrodontomys megalotis	4.8	10.9
Peromyscus maniculatus	4.0	9.1
Total	44.0	100.0

Yakima. Vegetation was similar in all areas, consisting mainly of the dominant common sagebrush (*Artemisia tridentata* Nutt.), somewhat less abundant black greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), and downy brome (*Bromus tectorum* L.). In 2a—2b *Chrysothamnus nauseosus* (Pall.) Britt. was also abundant. All sites were at least 500 yards from water and were typical of the desert. Their only use by man is as occasional sheep or horse pasture, and none had been so used for at least six months.

Mammals noted living in these areas were: Townsend ground squirrel (*Citellus townsendii*), estivating, not trapped; sagebrush chipmunk, (*Eutamias minimus*); Oregon pocket mouse, (*Perognathus parvus*); grasshopper mouse, (*Onychomys leucogaster*); harvest mouse, (*Reithrodontomys megalotis*); white-footed mouse,

(*Peromyscus maniculatus*); black-tailed jackrabbit, (*Lepus californicus*), not trapped; Nuttall cottontail, (*Sylvilagus nuttallii*), not trapped.

To estimate the rodent population in the sagebrush desert at this time of year the total number of each species caught in five quadrats, divided by five to get the mean number per quadrat, is multiplied by two to get the estimated population per acre. The estimated population of active rodents in one acre of sagebrush desert in the Yakima Valley during the months of August and September, 1941, is shown in Table 2.

To test the reliability of the nearly equal snap-trap and live-trap totals (57 to 53 individuals) the chi-square method may be applied to the six quadrat totals (28, 7, 22 against 26, 12, 15 individuals). The chi-square value of 2.714 indicates that a sample deviating this much or more from a 50:50 ratio might be expected about 27 percent of the time, a considerable degree of statistical reliability.

While trapping quadrat 3 it became evident that mice were taking the bait of the snap traps more readily than that of the live traps. It is probable that the more accessible bait on snap-trap pans attracted more mice than the bait inside the live traps. However, when there is no food more accessible than the live-trap bait, results tend to be equal for both types of trap.

The author was aided in various aspects of this investigation by Mr. Edmund S. Norton, Mr. George P. Downs, Miss Ethel Crum, Dr. Frances N. Clark, and Dr. Jean M. Linsdale.

SUMMARY

From five quadrats set in terrain typical of the sagebrush desert of the Yakima Valley, Washington, the following conclusions are reached:

1. Active rodent population during August and September, 1941, is estimated at 44 individuals per acre, composed specifically of: 2 *Eutamias minimus*, 32 *Perognathus parvus*, an occasional *Onychomys leucogaster*, 5 *Reithrodontomys megalotis*, and 4 *Peromyscus maniculatus*.

2. Similar quadrats of Sherman type and snap type traps produce similar results.

3. Sherman and snap traps may not be mixed in the same quadrat with the expectation of equal results since the bait of the latter is more attractive because it is more readily available.

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NOTES ON THE HABITS AND SIPHONAPTEROUS PARASITES OF THE MAMMALS OF WELLAND COUNTY, ONTARIO

By E. W. Jameson, Jr.

Over a period of several years, pertinent data were gathered on the life histories of several species of mammals at Point Abino, Welland County, Ontario. Observations and collections were made from November 24–26 and December 24–26, 1939; April 2–6, 1940; March 30–April 3, 1941; and August 23–September 22, 1942, at this locality and at irregular intervals elsewhere in Welland County.

Several of the typical habitats of this part of Ontario are represented in the immediate vicinity of Point Abino. The area considered is approximately 700 acres of which 75 percent is woodland, the remainder being grassland and beaches. The dominant woody vegetation is deciduous. Black oak (*Quercus velutina*), bitternut hickory (*Carya cordiformis*), black walnut (*Juglans nigra*), ironwoods (*Ostrya virginiana* and *Carpinus caroliniana*), beech (*Fagus grandifolia*), tulip tree (*Liriodendron tulipifera*), wild cherries (*Prunus serotina*, *P. virginiana*, and *P. pennsylvanica*), maples (*Acer saccharum* and *A. rubrum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*), and white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) are the trees most commonly seen. The dominant shrubs are spice bush (*Lindera benzoin*), witch-hazel (*Hamamelis virginiana*), dogwoods (*Cornus stolonifera*, *C. racemosa*, and *C. alternifolia*), wild black current (*Ribes americana*), and arrow-woods (*Viburnum dentatum*, *V. acerifolium*, and *V. trilobum*).

The area was trapped regularly, using small snap-back traps, steel traps, and live traps. The specimens were placed in white flannel bags immediately upon removal from the traps, and the fleas were saved for later identification. Stomachs were preserved in every instance and, although the numbers are insufficient for statistical analysis, they are used here to indicate the important food items.

In preparation of this paper I have received guidance from Dr. Edward C. Raney. Dr. Duane Isely gave me much assistance in the identification of the botanical material.

The account by species given below is not intended to be a complete list of the mammals of Welland County. The records serve to supplement the distributional studies by Miller (1897) and Saunders (1932), and the notes on the life histories may prove useful in compiling more comprehensive accounts of these species.

ACCOUNTS OF SPECIES

Didelphis virginiana virginiana Kerr. No specimens were taken, but residents spoke of its presence in former years.

Parascalops breweri (Bachman). On September 18, 1942, an adult male was taken in a surface runway of *Microtus* in a field of dense bluegrass. Its stomach contained four dipterous larvae and several larvae and one adult coleopteran. From it were taken three fleas, all of which were female *Ctenophthalmus pseudagyrtes* Baker.

Blarina brevicauda talpoides (Gapper). Short-tailed shrews are the most abundant and

ubiquitous of all the mammals studied, and were encountered in almost every area trapped. They were found most frequently in low level woods in *Pitymys* runways, and in grassland in *Microtus* habitat. The subterranean runways they occupy are found from just below the leaf mold to a depth of four inches or more. While passageways usually paralleled the surface, an occasional one would descend vertically. Moulting individuals were taken on August 23 and September 13. The most important single food item found in 28 stomachs was annelid remains; insect larvae and adults usually comprised the balance of the food eaten. The flea, *Doratopsylla blarinae* C. Fox, was often found on this mammal. *Hystricopsyllus gigas tahavauna* Jordan, and *Ctenophthalmus pseudagyrtes* Baker also occurred.

Myotis lucifugus lucifugus (Le Conte). Little brown bats are common and most often seen flying and feeding near water. At 8:15 p.m. on September 16, 1942, one male and two females were netted with a minnow net. The left half of the interfemoral membrane of one specimen had been torn for about 14 millimeters at a right angle to the tail vertebrae, but it had completely healed over. This injury had apparently not impaired the bat's flight for it was in good health. The common bat flea, *Myodopsylla insignis* (Rothschild), was taken from one specimen.

Procyon lotor lotor (Linnaeus). Raccoons are common and their tracks are often seen on woods trails and sand dunes. On September 5, 1942, a young male was trapped beneath the steps of a small building. Matted in the animal's coat were two dozen or more "burs" of enchanter's nightshade (*Circaea latifolia*). The stomach and intestine contained 162 stones of red-osier dogwood (*Cornus stolenifera*).

Mephitis mephitis nigra (Peale and Beauvois). Skunks are common about buildings and on the roads at night. During the summer months they commonly dig up lawns in search of insect food.

Vulpes fulva (Desmarest). Fox tracks are the commonest evidence of the animals' abundance. On September 3, 1942, at 6:45 p.m., I came within ten yards of a red fox asleep at the base of a small tree. At 5:00 p.m. on September 19, I saw a cross fox 40 yards from the above spot. It had been sleeping in a hollow "form" beneath a black oak. This hollow in the ground measured approximately one by two feet, and was surrounded by a rim of dead leaves. Almost every evening at dusk during the summer of 1942, residents saw a silver fox come out on a sandy beach and go to the lake to drink. This may have been an offspring of a vixen that was known to have escaped from a nearby fur farm in 1940.

Tamias striatus lysteri (Richardson). Chipmunks are common. A female taken on March 30, 1941, held six embryos which measured 9 millimeters. No animals trapped during August or September were gravid, but one taken on September 5 had been recently lactating. It seems most likely that this represents a second seasonal brood. From the cheek pouches of several animals stones of *Prunus serotina*, *P. virginiana*, and *P. pennsylvanica* were taken. An animal captured on September 5 had 24 sprouting seeds of *Prunus pennsylvanica* in its pouches. Remains of a deer mouse were in the stomach of another animal. Well masticated insect parts were in almost every one of the 15 stomachs examined, but the greater part of the stomach contents consisted of ground vegetable matter with an occasional scaly covering of a plant tuber or corm. None of the animals were parasitised by cuterebrids which were so commonly found in deer mice. Siphonapterous parasites collected from chipmunks were *Orchopeas howardii* (Baker), *Trichopsylla acerbus* (Jordan), *Epitedia wenmanni* (Rothschild), and *Tamiophila grandis* Rothschild.

Tamiasciurus hudsonicus loquax (Bangs). Red squirrels are common in all the woodlands. They are always to be found in the groves of hemlocks where the green cones form a major part of their summer diet. The squirrels cut off the cones at the base, and eat the seeds, dropping the bracts to the ground. During August and September, one can always find chickarees feeding in this manner, while 20 yards away gray squirrels might be feeding in the tops of beeches. The seed coats of staghorn sumach were found in the stomach of one September specimen. Each of two males taken during September was host to six fleas, *Orchopeas howardii* (Baker).

Sciurus carolinensis leucotis (Gapper). In contrast to other nearby areas, gray squirrels

at Point Abino are abundant and easily observed. They are often active about buildings. In the fall they gather the nuts of black walnut and the acorns of black oak. The mast from bitternut hickory and witch-hazel is also much sought after. On September 4, at 9 a.m., three gray squirrels were feeding silently 40 feet from the ground in a beech tree. Not infrequently they would drop nuts, thus making a considerable preseasonal supply available to the less arboreal rodents.

Glaucomys volans volans (Linnaeus). One male was taken in a trap at the base of a large hard maple on September 20. From it were taken 5 fleas, *Orchopeas howardii* (Baker).

Peromyscus maniculatus bairdii (Hoy and Kennicott). On April 3, 1941, a male prairie deer mouse was taken at the edge of a deciduous woods near an open field. This was the only time it was taken, and it was then during a high *Peromyscus* population. This species probably occurs on the sandy shores of Lake Erie, but no specimens were collected there.

Peromyscus leucopus noveboracensis (Fischer). Deer mice were always to be found in the woodlands and often enter homes, especially during the winter months. Late in the summer of 1942, their numbers were very low as compared with what they were during other trapping periods. Coincident with this low population was an infestation of *Cuterebra* sp. in 80 percent of the animals collected. The mice averaged 1.5 larvae per animal while as many as four were found in one host. Several infested animals were kept alive until the larvae emerged. The mice ate them during or soon after emergence, however, and the only way a full grown larva could be obtained was to kill the mouse just as the larva was emerging. All the full grown larvae were in the inguinal region, but in no instance were any mice emasculated. Infested females were found bearing embryos and infested males were found to have testes of normal size. The larvae in two animals under observation required 3 and 6 days to emerge after they first became visible. During the time of emergence of the parasites the deer mice walked with an awkward gait. One deer mouse was found in the stomach of a chipmunk which in view of the different activity periods of the two animals might lead one to believe that the mice are seriously handicapped by these parasites. The mass of the stomach contents consisted of ground vegetable matter. Most of the stomachs also contained adult insect remains, and two contained feathers of small birds. An occasional siphonapterous parasite, *Orchopeas leucopus* (Baker), was found.

Microtus pennsylvanicus pennsylvanicus (Ord). Meadow mice are found in open fields where they make their runways under a dense protection of bluegrass and horsetail (*Equisetum arvense*). They were also trapped near still water where their runways in stands of broad-leaved cattail were not so well defined. Meadow mice were hosts to fleas of the species *Ctenophthalmus pseudagyrtes* Baker.

Pitymys pinetorum scalopsoides (Audubon and Bachman). This small mouse, which has been collected very few times in Ontario, was taken twice during September 1942. Both were in runways that were being used by *Blarina*, *Peromyscus leucopus*, and probably *Parascalops*. The tunnels were in the soft dirt in a low damp woods where deciduous trees dominated. Both were hosts to the same fleas that commonly parasitise other mammals of the same habitat, namely *Ctenophthalmus pseudagyrtes* Baker. Perhaps persistent trapping would show this animal to be more common and widespread in southern Ontario.

Ondatra zibethica zibethica (Linnaeus). Muskrats are locally abundant in a small marsh where they build their homes in the banks of a drainage ditch.

Mus musculus musculus Linnaeus. This introduced species was not found to be locally common, but it was taken occasionally in and about houses.

Rattus norvegicus (Erxleben). One male was taken under a cottage.

Sylvilagus floridanus mearnsi (Allen). Cottontails are common. One young male taken September 4 had one flea, *Tamiophila grandis* Rothschild. One adult female trapped September 19 had a nearly full grown larval *Cuterebra* sp. in its left shoulder.

Odocoileus virginianus borealis (Miller). Deer are usually present at point Abino during the winter months when it is believed they come across Lake Erie on the ice. During the summer of 1942, at least two deer remained to breed for the first time in many years.

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REMARKS ON *MYOTIS OCCULTUS* IN CALIFORNIA

BY KENNETH E. STAGER

Since the description of the *Myotis occultus* by Hollister in 1907, all published accounts of this interesting and rather rare bat that have come to my attention fail to give any information as to its roosting habits or the type of situations selected for its diurnal retreat. Most writers mention that specimens were collected by shooting them as they foraged among stands of cottonwoods or over open bodies of water.

My first acquaintance with *Myotis occultus* came on August 16, 1937, in the Riverside Mountains, Riverside County, California. On this date I entered a large abandoned copper mine in search of bats and, while making my way along the main haulage tunnel, I collected an adult male *Myotis occultus* from a roost in a shallow pocket in the rock wall, 6 feet above the floor of the tunnel and approximately 100 feet from the mine entrance.

I did not encounter the Hollister's bat again until April 30, 1939, at which time a large number of *Myotis occultus* were turned over to me dead by Mr. William Lasky, an amateur herpetologist. According to Mr. Lasky, the bats were encountered while he was in search of reptiles in the Lower Colorado River Valley in the vicinity of Blythe, California. Following directions given me, I located the colony on May 14, 1939. The colony, consisting of approximately 2,000 bats, was made up of three species, namely *Myotis occultus*, *Myotis yumanensis yumanensis*, and *Tadarida mexicana*, with *Myotis occultus* making up approximately 40 percent of the total.

For their roost the bats had chosen a large bridge. At a point where the horizontal timbers which support the roadbed of the bridge are bolted together on top of the piers, spaces one inch wide and twelve inches square are formed, due to the timbers being held apart from one another by washers one inch thick. The size of the bridge provides approximately 400 of these vertical crevices and it was here that the bats were found to have their diurnal retreat. Quantities of excrement showed that the majority of these spaces are utilized at some time or another, but the most desirable ones seem to be those in the center of the piers, as far away from the sides of the bridge as possible.

In the semi-darkness of these spaces the bats congregate in large numbers, with each space accommodating 20 or 30 individuals. Here, as is often the case, a social delineation was noticeable, with the *Tadarida* roosting by themselves

and the other two species of *Myotis* roosting together. Some spaces, however, were found to harbor only *Myotis occultus*, while others held only *Myotis yumanensis yumanensis*. When disturbed, *Myotis occultus* became restless and oftentimes left its roosting place and flew to other sections of the bridge.

From information now available it may be said that *Myotis occultus* is known to occupy the roost from as early as April 20 to as late as August 13, but subsequent observations at earlier and later dates should extend the period of time the species is known to be present in California. A visit to the roost on February 17, 1940, failed to disclose bats of any species.

An examination for ectoparasites on the specimens collected showed them to harbor two species of bat fleas, *Myodopsylla gentilis* Jord. & Roths. and *Myodopsylla collinsi* Kohls. (Identifications by Glen M. Kohls, U. S. Public Health Service.)

A total of 63 specimens have been taken from the colony to date, with 21 being placed in the Los Angeles Museum collection and 42 in the Stager collection, also at the Los Angeles Museum. Only females were found in the roost between April 20 and June 2, but on August 13 both sexes were found together, with 7 of the 13 specimens collected at that time being males.

Due to the scarcity of information on the abnormal dentition of this species, the following remarks and observations seem justified at this time. *Myotis occultus* is well known for the peculiar tendency it shows towards crowding and elimination of the small premolars. Hollister, in his description of the species (Proc. Biol. Soc. Washington, vol. 22, p. 43, March 1909), first pointed out the presence or absence of the middle upper premolar (pm^3) and stated that it was missing in one of his two specimens and present in the other. Grinnell (Univ. Calif. Publ. Zool., vol. 12, p. 265, March 1914) later corroborated Hollister's findings by showing that 50 percent of known specimens collected (which totaled 8 at that time) showed this remarkable aberrancy from the norm in the genus *Myotis*. Sometime later, Miller and Allen (Bull. U. S. Nat. Mus. 144, p. 99, April 1928) while examining a series of 27 specimens, including the two taken by Hollister and the six taken by Grinnell, found that the second upper premolar was absent 17 times in 24 specimens and, if present, it usually was pushed out of the tooth row into the angle between the first and fourth premolars where it was not visible in side view. They also found that where the second premolar is normally present in the lower jaw of *Myotis*, it was lacking in 2 out of 24 skulls of *Myotis occultus* examined. If present, it may be crowded inward from the toothrow, or it may stand in the row closely pressed between the other two premolars.

In addition to the above information regarding this aberrancy as shown by previous workers, a study of 67 skulls of *Myotis occultus* (43 from Stager collection and 24 from Los Angeles Museum collection) sheds still further light on this dental abnormality. Examination of this series showed that in 31 skulls the second premolar of the upper jaw was missing on both sides, in 8 it was missing only on the right side, and in 6 it was missing on the left side, thus making it fully present in only 22 specimens.

An examination of the premolars of the lower jaw shows the second premolar to be absent only once out of the 67. It might be interesting to point out that in the skull where the second premolar is missing on both sides of the lower jaw, it is also missing on both sides of the upper. Miller and Allen, in their discussion on the subject, fail to mention the absence of the premolar on only the right or left side, so I assume that in the specimens examined by them they found the premolar either present or completely absent on both sides.

A still further departure from the norm is exhibited by one skull of the series (no. 846 Stager coll.). In this case two well developed canines are present on each side of the upper jaw. The extra canine on the right side is crowded inward and lies forward of the normal one, while on the left side the extra tooth lies inward and posterior to the left canine. The second upper premolar is missing on both sides. This case of a second set of upper canines seems to have no real significance other than to point out further the instability of the dentition in this species.

To summarize briefly the above data, it has been shown that of the total of 91 skulls examined, 62 have shown a tendency toward elimination of the second premolar as compared with 29 showing a normal complement of teeth for the genus.

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A SECOND SPECIMEN OF TRUE'S BEAKED WHALE, *MESOPLODON MIRUS* TRUE, FROM NORTH CAROLINA

By H. H. Brimley

Early in March 1940 word of a small toothless whale ashore between Gull Island and Oregon Inlet, Dare County, North Carolina, reached the Museum. It was a week or so later, however, before any member of our force was able to look into the matter when H. T. Davis, Director of the Museum, made the trip.

The specimen proved to be an adult female ziphioid whale, 17 feet in length and it was found to contain a well-developed foetus about ready for delivery. The foetus measured 7 feet 2 inches in length with an estimated weight of 175 to 200 pounds. This was brought to the Museum and preserved in fluid after plaster casts had been made of the body, from which a life-sized model has been prepared.

The head of the adult, together with the tail and the flippers, was also brought back for casting, and all the bones of the specimen later were roughed out and placed in a sand-box for maceration. As the two teeth were deeply imbedded in the tough tissue of the gums, they were left *in situ* during the maceration period, being later removed and photographed.

As there was some doubt as to the identity of the specimen, the skull and teeth were submitted to Remington Kellogg, who identified the specimen as *Mesoplodon mirus* True, True's beaked whale, the type specimen of which was de-

scribed by True in 1913 (Proc. U. S. N. M., vol. 45, p. 651) from a stranded specimen found on Bird Shoal, Beaufort Harbor, North Carolina, on July 26, 1913.

Because the whale had been on the beach for more than a week when Mr. Davis arrived on the scene, its coloration in life could not be determined with any exactitude. The brownish-black of the upperparts, however, probably had undergone but little change. The underparts were lighter, but not white.

The symmetrical curved line of the large blow-hole and the V-shaped grooves of the throat area are noticeable characteristics of the head, as is the somewhat projecting lower jaw. These features are indicated in the accompanying illustrations.

In situ, the foetus was doubled back on itself, left side to left side, the distal portion making a quarter turn in the region of the caudal peduncle so that the caudal fin fitted snugly against the throat, with the individual flukes curved up close to the sides of the head. The foetus was facing backwards in the body of the parent, towards the genital opening.

On March 30, 1940, Kellogg wrote me that at that time only eight specimens of this species had been recorded since it was originally described by True.

SOME MEASUREMENTS AND OTHER DATA

Sex, female, with well-developed foetus *in situ*.

Length	17 feet
Greatest depth of body	42 inches
Estimated weight	2,500 to 3,000 pounds
Length of head	35 inches
Depth of head at base	24 inches
Width of head at base	18 inches
Width of flukes	42 inches
Flippers	6 x 14 inches
Height of dorsal	9½ inches
Length of dorsal at base	15½ inches
Eye to tip of snout	25 inches
Forward edge of dorsal to base of flukes	54 inches

Teeth: Not showing above gum, the two being hidden under about an inch of tissue. They pointed almost directly forward; are triangular in shape, much flattened horizontally, and situated close to the tips of the mandibles.

Total height of left-hand tooth	52 mm.
Width at base of left-hand tooth	28 mm.

The right-hand tooth measures about 1 mm less in both dimensions.

The following notes and measurements of the skull were made by Kellogg, with permission to use them in connection with this paper:

Mesoplodon mirus

The jugal forms most of the maxillary notch viewed from above; the lachrymal constitutes the tubercle at the preorbital end of the supraorbital process of the frontal.

The antero-posterior extension (along median line of vertex) of expanded hinder end of premaxillary is reduced to a thin wedge-like strip, narrowed posteriorly. Antero-posterior diameter of right premaxillary on vertex, 84.5 mm.

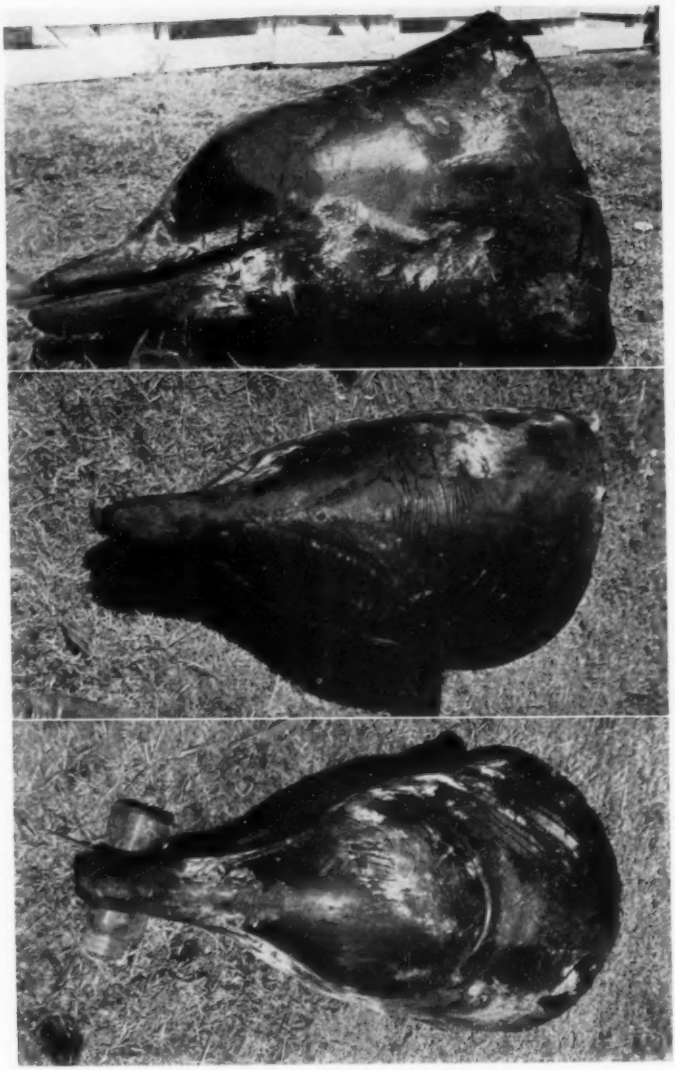

PLATE 1

Head of adult True's beaked whale: *Top*, Profile; *middle*, Ventral view; *bottom*, Dorsal view

PLATE 2
Foetus of True's beaked whale

Depressed triangle on each premaxillary (located between choanae and premaxillary foramen) distinctly flattened and not "dished in."

Expanded extremity of right premaxillary larger (wider and thicker) than left. Between choanae and premaxillary foramen, the right premaxillary is likewise wider than the left.

Nasals larger than those of adult female (No. 90053, A.M.N.H.). Antero-posterior diameter of right nasal, 75 mm.; of left, 75.5 mm. Transverse diameter of right nasal, 26.5 mm.; of left, 19 mm.

V-shaped wedge on vertex formed by the frontals; width of the two frontals combined at base posteriorly, 47 mm.; antero-posterior diameter of same medially, 36.8 mm.

Antero-posterior diameter of right supraorbital process of frontal, 165 mm.; of left, 165 mm.

Distance between inner angles of maxillary protuberances, 145 mm. Crest on maxillary protuberance is placed obliquely.

Longitudinal ridges on orbital plates of maxillaries (extending from maxillary [antorbital] notch to almost level of hinder end of orbit) well marked.

MEASUREMENTS OF THE SKULL (IN MILLIMETERS)

Condylobasal length of skull (terminal 30± mm of rostrum missing)	802+
Height, vertex to inferior border of pterygoids	312
Height, vertex to basisphenoid	211
Width at center of orbits	349
Width across preorbital angles of supraorbital processes	352
Width across postorbital angles of supraorbital processes	374
Zygomatic width	357
Distance between outer margins of occipital condyles	132
Rostrum, length from level of maxillary (antorbital) notches to tip	510+
Rostrum, width between bases of maxillary (antorbital) notches	207
Rostrum, width at middle	70
Distance from tip of rostrum to hinder end of pterygoids	643+
Least distance between inner margins of maxillaries at the vertex	46.5
Greatest distance between outer margins of expanded proximal ends of premaxillaries	162.5
Least distance between outer margins of premaxillaries opposite choanae	114.5
Distance between outer margins of premaxillaries opposite premaxillary foramina	66.5
Greatest distance between outer margins of choanae	55.5
Least distance between maxillary foramina	92.5
Distance from posterior border of maxillary foramen and end of maxillary protuberance	69
Greatest height of temporal fossa, externally	77
Breadth of skull across exoccipitals	308
Antero-posterior diameter of right nasal	75
Length of portion of vomer visible on palate	152.5
Greatest length of mandible	right, 673+; left, 669+
Length of symphysis	right, 188+; left, 175+
Greatest height of mandible at coronoid process	right, 117+; left, 123.5

State Museum, Raleigh, North Carolina.

EXPERIMENTAL MASSETERECTOMY IN THE LABORATORY RAT

By Loring W. Pratt

This work was undertaken, with the advice of A. Brazier Howell, to determine the effects of unilateral muscular damage upon growing bone and upon the symmetry of the skull. Experimentation of a similar nature has been done in one or two instances, such as the work on section of the temporalis in dogs by Anthony (1903), and by Anthony and Pietkiewicz (1909), but without very noteworthy results.

The laboratory rat was chosen for study because it is easy to obtain, numerous young are available upon the day of birth, and much can be done that would not be feasible in larger mammals.

The operations were all done under anesthesia, and every care was taken to provide for the comfort of the animals before, during, and following operations. Aseptic technique was not used because, for some obscure reason, it is unnecessary in the rat and no case of postoperative infection ensued. The postoperative care was far superior to that provided the average laboratory rat, as larger, less crowded cages were used and they were given special and particularly nourishing foods that would be easy to eat.

The rat does not have a true glenoid fossa, but has much room for lateral and propolinal motion, a feature in common with the asymmetrical primate skulls studied by Howell (1925). In this respect rodents such as the rat are more comparable to primates than to carnivores.

Methods.—In conducting a study of the effect of masseterectomy in very young rats, several different procedures were tried. In the first, rats one day old were chilled on ice until movement nearly ceased, and were then subjected to operation (incision shown in fig. 1). This was found to be unsatisfactory, as considerable bleeding resulted, and it is almost impossible to control hemorrhage in the new born rat. In the second method, after chilling, hot dissecting needles were tried for cautery, and in some instances the muscle was destroyed by searing. This technique was not satisfactory as the wound was in the nature of a deep burn, with the gaping edges healing slowly.

The third method was evolved from the first two. Rats about a week old were used and operated on while an assistant gave ether anaesthesia. The skin of the cheek was incised from below the zygomatic arch, just below the eye, to the angle of the jaw (fig. 2). The skin flaps were retracted, and the external jugular vein located and ligated with silk inferior to the masseter. The masseter was then reflected from the mandible by means of blunt dissection and removed, except for the part passing through the infraorbital foramen. The internal maxillary artery occasionally gives trouble in this reflection, but ordinarily no excessive bleeding is encountered. In some specimens, the zygomatic arch was interrupted by snipping out a small piece of the bone. After this, shreds of muscular tissue found in the incision were removed by fine pointed tweezers and small scissors. This is a rather radical operation and involves

considerable trauma to the tissues of the face and cheek. There is some danger of injury to the facial nerve, but in no case has any deficiency been observed that could be attributed to its section or other injury. The wound was rinsed with warm normal saline solution and the skin flaps approximated with interrupted sutures.

Results.—Recovery following the surgical procedures is remarkable. The young rats return to suckling within one half hour after they have revived, and, if the mother accepts them, they stage a very rapid recovery. Within one day they frequently lose all signs of inconvenience caused by the operation.

It was found necessary either to operate on all individuals of a litter or to destroy the intact young, for a mother is extremely likely to kill what she considers to be an injured young one, whereas she will not molest it if all the others are equally affected. An additional reason for treating the whole litter is that babies handicapped by the operation are able to compete with one another, but not so well with those that are normal.

FIG. 1. No. 1. Original type of incision; no. 2. Improved type of incision.

Attrition of the incisors begins a few days after eruption and by 19 to 21 days their normal occlusal surfaces are formed in normal rats (Addison and Appleton, 1915). As normal extrusive growth continues after the operation, it was found necessary to cut the incisors every week and a half or two weeks in order to prevent them from interfering too seriously with feeding. The upper incisors grow about 2.2 mm, and the lower incisors, about 2.8 mm, per week (Addison and Appleton, 1915). The teeth were cut a little shorter than they would wear under normal attrition and allowed to grow slightly longer than normal.

After weaning, a small bottle of milk was attached to the animal's cage, and soft foods, in addition to a diet of meal, were fed. The meal was a mixture of fish meal, peanut meal, soya bean meal and standard middlings, with milk meal included in a few mixtures. Frequently meat meal was substituted for fish meal, and the two mixtures were alternated at regular intervals. At least twice a week, green vegetables were fed, and it was found that such greens as the tops of carrots could be readily eaten by the animals.

The functional freedom of the animals was very interesting to observe, and the variety of food that they were able to eat was surprising. In rat number 1,

the lower teeth were allowed to grow until they reached a position lateral to and just below the right eye (Pl. 1, nos. 7, 8, 9). These were allowed to grow because they did not interfere with the upper lip, and also because the animal showed great dexterity in eating things that might be thought beyond her ability. She ate meal, like any of the other treated animals, by picking up a handful and putting it in her mouth. She seemed to have complete freedom of use of her molars, and only the difficulty of getting food into the mouth was observed. She ate bread, either dry or soaked in milk, both the white and yolk of cooked or of uncooked eggs, bananas, and carrot tops or broccoli with evident relish. Often, food was broken up or shredded by the front feet before it was eaten. The milk diet was the easiest for her to obtain. This particular animal, number 1, successfully raised a family of eight large, plump and well nourished babies with no appreciable difficulty and without resultant emaciation. When she was killed, it was found that she was again pregnant.

While the animals were alive, the functional deformity varied with the specimen. In all probability, this variation was due largely to differences in the exact amount of masseter tissue removed. As has been described, the part of the masseter originating from the medial surface of the zygomatic arch, and that passing through the infraorbital foramen, was left intact, because of the danger of hemorrhage if this was disturbed. If little of the masseter was left, the deformity became so extensive that the lower incisors would move far enough laterally to avoid interference with the upper lip on that side. If more of the masseter were left, the resulting lesser distortion meant more interference with the upper lip. Should this interference occur, it would be very painful for the animal, and for this reason the lower teeth of most of the specimens were cut regularly. Only in one instance, that of rat number 1, were the lower incisors allowed to grow freely. In no case were the uppers allowed to grow to a point where they would become painful.

The upper incisors were deflected somewhat, so that if they had been allowed to grow, they would have perforated the palate asymmetrically. The deflection of the lower incisors was the most significant feature of this change, as complete malocclusion left the upper incisors free to grow without the restraining effect of normal attrition and continued growth would have allowed them to complete their circle, and to perforate the palate.

Perhaps the best picture of the extreme result in life can be seen from the photographs of rat number 1 taken immediately after death (Pl. 1, nos. 7, 8, 9). These show dorsal, lateral and ventral views of the rat, to indicate the profound changes in external appearance brought about by this operation. This rat was unilaterally masseterectomized and the zygomatic arch was interrupted on the same side.

Autopsy of these animals revealed that the rats were well nourished, appeared to be in excellent health, and no pathology was observed outside of the operated region. In each animal at least partial destruction of the masseter was found. The mandibular insertion was completely gone from the angle and part of the ramus, to a point half way between the ventral margin of the mandible and the

zygoma. Above this point, in most specimens, some masseteric fibers were found, and it was observed that these tissues had a distinctly darker color, coarser fibers, and difference in the elasticity of the muscle that was thought to indicate a marked hypertrophy of those fibers remaining. Where one external jugular was ligated at operation, it was observed that collateral circulation with the contralateral jugular was readily established.

In beginning a detailed consideration of the skulls of the animals prepared as above, one or two important points should be noted. The skulls were prepared by dermestid larvae, and bleached with hydrogen peroxide. All original rela-

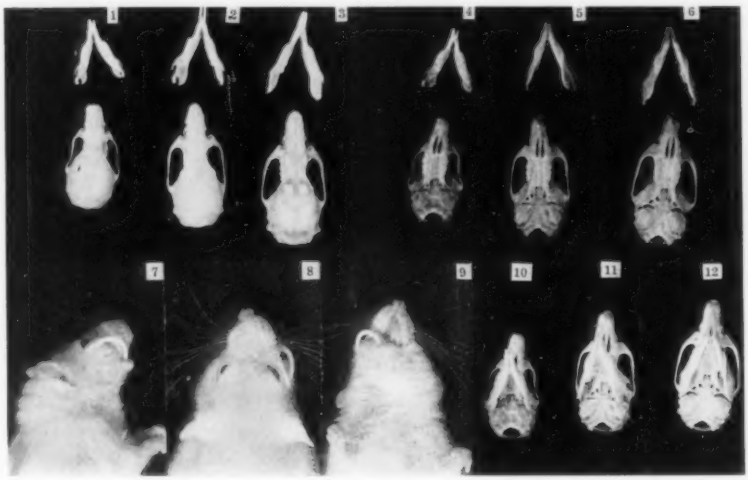

PLATE 1

Nos. 1, 4, 10. Dorsal and ventral views of skull of rat no. 2; nos. 2, 5, 11. Dorsal and ventral views of skull of rat no. 3; nos. 3, 6, 12. Dorsal and ventral views of skull of young adult, normal rat; nos. 7, 8, 9. Lateral, ventral and dorsal views of rat no. 1, taken just after death.

tions were determined by studies upon the dried head before contact of fluids could soften the mandibular symphysis.

The bizarre effects produced in the incisors in some of the specimens, are secondary to the study, but the reason for this great extrusive growth must be kept in mind and forms the primary consideration here.

Attention will first be given to the changes produced in the animal showing the most remarkable variations from normal. This rat, number 1, a tan hooded female, was operated on when one day old, at which time unilateral masseterectomy was done, and the zygomatic arch of the same side was interrupted. The rat grew normally, developed into an adult, delivered and raised a litter of eight babies, and again became pregnant shortly before her death.

In this skull there have been asymmetrical changes, probably primarily in

the mandible (Pl. 2, nos. 2, 4, 6). There is considerable shortening in the long axis of the mandible, least between the condyle of the mandible and the incisor and greatest (16 percent) between the tip of the coronoid process and the alveolus of the incisor.

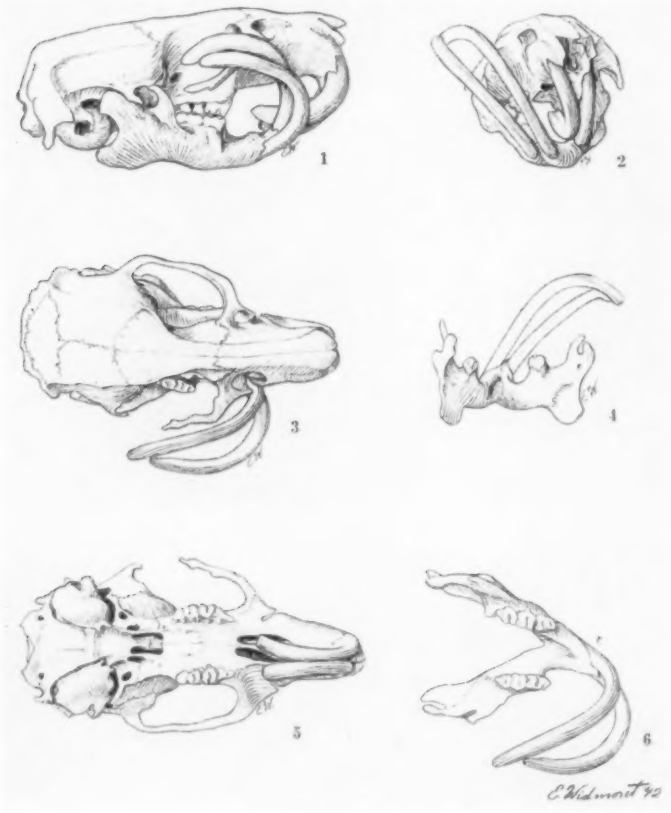

PLATE 2

Nos. 1 and 3. Lateral and dorsal views of the skull of rat no. 1; no. 2. Anterior view of skull of rat no. 1; no. 4. Posterior view of mandible of rat no. 1; no. 5. Ventral view of cranium of rat no. 1; no. 6. Dorsal view of mandible of rat no. 1.

Vertical measurements on the jaw reveal an increase in the depth of the mandible on the operated side. As these measurements were taken from the occlusal surfaces of the crowns of the molars, it is likely that this difference is occasioned by the molar malocclusion, resulting in more attrition of the molars on the unoperated side of the skull than on the other. Other vertical propor-

tions most markedly changed are the vertical depth of the neck of the condyle, which is reduced almost 19 percent as compared with that on the unoperated side. The distance between the angular and the coronoid processes is also reduced by nearly 9 percent. The last two are regarded as significant changes and they certainly are definite reductions in the mass of osseous structure developed in a region not under the stresses and strains of normal life.

The incisor capsule is much reduced in size, and does not show the definition nor the vertical length evident on the unoperated side. There is only a faint masseteric ridge visible on the inferior border of the operated side, in direct contrast to the unoperated side. There is some slight indication of dam age to the surface of the bone, as though the periosteum had been disturbed at the time of operation, resulting in an uneven surface in the scraped area.

Probably the most important mandibular change is in the angle of the mandibular symphysis. This can best be seen in Plate 2, no. 3. The symphysis angle has deviated from the perpendicular toward the operated side, as indicated by the change in the angle of the lower incisors. In addition, slippage has occurred in the ligamentous symphysis, resulting in a change of the normal symmetry by a relative rise in the mandible of the operated side. This is all due to the need for accommodation to the mandibular shortening and inactivity of the operated side of the animal.

The major change in the mandibular position in these animals seems to be due to the combined influences of the masseter and the slight interference of the lower incisors. The effect of the intact masseter upon the unoperated side is to pull the ramus of the mandible up under that side of the skull. This causes the mandibular symphysis to rearrange its angle somewhat, resulting in a deflection toward the operated side. As soon as the lower incisors rub against the operated side of the animal's head, the masseter pulls upon the lateral side of the unoperated ramus, and there is set up a group of forces that tend to increase the mandibular angle. In this way distortion of the mandibular symphysis is maintained throughout the life of the animal. The constant pull of the temporalis on the operated side has resulted in a more vertical coronoid process than is found on the unoperated side. This change in angle on the unoperated side, and its divergence, is due to the rearranged angle of the mandible.

The cranium shows considerable distortion (Pl. 2, no. 5). The right zygomatic arch is interrupted for about 0.5 mm. There is no other bony loss, and all changes are rearrangements in the proportions of the bones and their relations to one another. There is considerable deflection of the skull, rostral to the coronal suture (Pl. 2, nos. 2, 3), toward the unoperated side. This has resulted in a deflection of the premaxillae toward the unoperated side. As the upper incisors pass the point at which normal attrition would limit their length, they gradually diverge so that their continuation would cause one to pass through the palate, probably at the anterior palatine foramen, and the other up into the surface of the maxilla anterior to the molars and below the infraorbital foramen (Pl. 2, no. 5).

Aside from the changes occasioned by the torsion of the rostral part of the skull, there are no changes of note in the cranium of this animal.

Due to the considerable deviation of this specimen, it is felt that there are two chief factors contributory to the extreme amount of distortion. These are the interruption of the zygomatic arch and the very early date at which the animal was treated. The interruption of the arch may have resulted in two possible changes. The distortion may be due to a "release" phenomenon, or it may be due to the fact that when the arch was interrupted, more of the masseteric tissue was destroyed. The infraorbital origin of the muscle was then destroyed more completely than in the others, with the result that the spasmodic, longitudinal contractions on the other side of the skull allowed the rostrum to be deflected in the direction in which tension was greatest.

The other chief alteration in the animal was in the occlusal surfaces of the molars. These reflect the stress and strain of the muscles. The molars in the normal rat less than a year old are not badly worn and show their cusps clearly. Normal attrition of the molars produces wear in a very different way from that found in masseterectomized animals. The asymmetrical attrition of the molars is well seen in Plate 2, no. 6.

The other experimental animals showed much the same deformities, differing only in degree. Rat number 2 was operated on when 6 days old and died when 43 days old. It shows the most profound change obtained in any instance in the rostral part of the skull (Pl. 1, nos. 4, 10, 11). The skull is still immature, and for that reason it is rather difficult to use as a basis for thorough study. The same trend in alteration of bony proportions is found as in rat number 1. There are variations in degree, but no essential differences.

Rat number 3 was unilaterally masseterectomized when 6 days old and lived until 43 days of age. Distortions in this skull follow the same pattern as in numbers 1 and 2 with the exception that rostral distortion is much less, and the mandibular symphysis has a more normal angle (Pl. 1, nos. 2, 5, 11).

Rat number 4 exhibits the same trends as were described in the case of number 1. This rat was unilaterally masseterectomized when 7 days old and died when 18 days old. It was raised in a litter of normal animals and was unable to meet the competition of the others.

It is well known that tension or impact stimulates linear growth of bone in the opposite direction, and that a process will tend to grow at a right angle to muscle pull, although the results are variable. Part of the growth of a process is usually ontogenetic and part inherited.

In endeavoring to interpret the deformities of the masseterectomized rats in terms of the above tenets, I may first consider the reduction in distance between the angular and coronoid processes of the mandible. It is thought that this may be attributed to the lack of tension upon the angular process and it may be pointed out that this also accounts for the reduction in vertical thickness of the neck of the mandible, on the operated side. The slight increase in the total length of the mandible may be accounted for by the fact that attrition of the incisors takes place for some time in these animals, and that complete malocclusion occurs on the unoperated side first. This exposes the operated side to attrition, or impact, for a longer period of time, which accounts for its slight increase in length. Reduction of the bony eminences may be seen in the lessened depth

of the masseteric ridge, which has no muscle to pull against it. This would seem to favor the ontogenetic factor in the development of processes in bones. The fact that it is not totally absent could be accounted for largely by the fact that hereditary development seems to play a prominent part in this process.

From this, it may be seen that the laws of bone growth are illustrated by the distortions seen in these skulls, and that some of the deformities may be explained in terms of principles already understood.

The author gratefully acknowledges the cooperation and assistance of Miss Elinor Widmont of Art as Applied to Medicine of the Medical School of Johns Hopkins University in making the drawings for this paper, and in arranging the plates.

Conclusions.—This study indicates that experimental masseterectomy causes asymmetrical development in the skull of the laboratory rat. Mandibular development is retarded by experimental masseterectomy. Malocclusion is developed by experimental masseterectomy. Long mandibular proportions are little changed. Vertical mandibular proportions are most changed. Rostral torsion is muscular rather than a "release" phenomenon when the zygoma is interrupted

SUMMARY

Unilateral masseterectomy was produced in the laboratory rat at an early age, and the young thus altered were raised to various stages of development. The amount of masseteric tissue removed, coupled with the presence or absence of a complete zygomatic arch, produced noteworthy changes in the development of the mandible, the angle of the mandibular symphysis, the attrition of both the molars and the incisors, and the development of the rostral region of the skull. Bone growth seems definitely related to the presence of muscular tissue actively pulling upon it.

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Henry Strong Denison Scholar for 1942–43.

A STUDY OF INDIVIDUAL VARIATION IN *MICROTUS PENNSYLVANICUS PENNSYLVANICUS*

By Olive B. Goin

It is hardly necessary to state that in any series of animals taken from the same locality there will be a certain amount of individual variation, but in most cases little is known of the extent of this variation, especially in the smaller mammals. J. A. Allen (1894) published an account of a study of such variation in *Neotoma micropus* dealing chiefly with differences in size and relative proportions due to age. A. B. Howell (1924) has a similar paper on *Microtus montanus yosemite*, and Dice (1932) and Sumner (1920) have both worked with *Peromyscus*, although they have been more concerned with differences in populations due to geographical variation. An account of variability in the Platyrrhine monkeys was published by Schultz (1926). As yet, however, we have little knowledge of the range of variation that may occur in a group of mammals living in one locality and consequently subject to closely similar environmental effects. Such knowledge is essential to the study of geographical variation in relation to the formation of subspecies and is thus fundamental to an understanding of the processes of evolution. This present study was undertaken with the idea of obtaining some information regarding variation in a representative series of the Pennsylvania meadow mouse, *Microtus pennsylvanicus pennsylvanicus* (Ord).

I wish to express my gratitude to the late Dr. H. H. Collins of the University of Pittsburgh for his many helpful suggestions and criticisms. I also wish to thank Mr. J. Kenneth Doutt of the Carnegie Museum, who, with Mr. William LeRoy Black, collected the specimens here reported on, and who has been unfailingly kind and helpful to me throughout. I am indebted to Mr. John J. Burke for many pertinent suggestions in the interpretation of variation in the molar pattern. Dr. H. B. Sherman of the University of Florida read the entire manuscript and has offered a number of helpful criticisms. Finally I wish to thank Dr. T. H. Hubbell of the University of Florida for editing the manuscript.

The specimens studied, which are now in the collection of the Carnegie Museum, were taken in Pymatuning Swamp, Crawford County, Pennsylvania. Collections were made in 1932 from March 31 to May 29, September 17 and 18, October 2 to 8, October 30 and 31, and on February 17 and 18, 1933. At that time, before the construction of the Pymatuning Dam and Reservoir, Pymatuning Swamp was a wooded bog, roughly crescentic in shape, extending northward from Adamsville past Hartstown and Shermansville almost to Linesville, and then running west and northwest to Espyville, and in a narrow belt to Westford and further south. It was about 15 miles in length, and varied from one to three miles in width. Most of the trapping was done in the region west and southwest of Linesville, and in the vicinity of Hemlock Island, an elevated knoll that was probably once an island in the glacial lake that formerly occupied the region of the swamp.

One hundred and twenty-nine specimens of *Microtus p. pennsylvanicus* were

taken, 69 males and 60 females. Only adult specimens with skulls in good condition are included in the measurements. These number 56 males and 48 females. Certain skulls were slightly damaged so that some of the measurements could not be taken on them; therefore not all of the series of measurements include the entire series of specimens. The external measurements and the presence of embryos were recorded at the time of skinning. The study skins

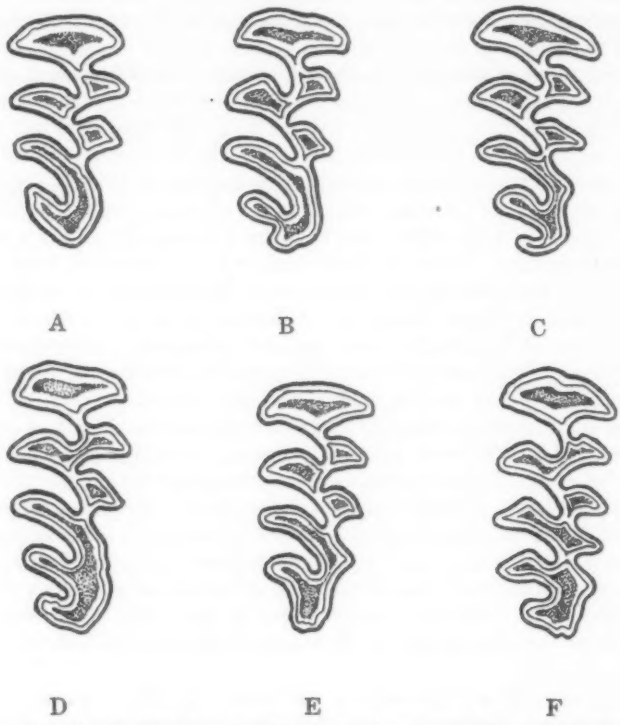

FIG. 1. Variation in third upper molar of *Microtus p. pennsylvanicus* showing approach to the *M. chrotorrhinus* type. A. Normal *pennsylvanicus* molar with four inner and three outer salient angles. B, C, and D. Stages in development of fifth inner salient angle. E. Rudiment of fourth outer salient angle. F. Normal *chrotorrhinus* molar with five inner and four outer salient angles. Drawn by W. L. Brudon.

were examined for coloration and for evidences of molt; measurements were taken on the skull; and variations of pattern of the molar teeth were studied.

There is little obvious difference in the color of the specimens. Some of them appear grayer than the others, but this is due to the fact that in these the pelage is more worn so that the light terminal bands of the hairs have been lost and the dark plumbeous bases are exposed. Specimens with an unworn pelage are

browner. Molt is not evident on the surface as it is in *Peromyscus* but may be seen by blowing back the hairs of the coat so that the dark tips of the incoming hairs are exposed. No definite molt pattern was observed. Eight of the 53 individuals taken in April were in process of molt, as were 9 of the 25 taken in May. Four young specimens caught in October were assuming the adult coat. Time of molt is probably largely determined by the age and physical condition of the animal, and since, as Bailey (1924, pp. 528–531) indicates, there is no definite breeding season for *Microtus*, there appears to be no definite season for change of pelage.

Twenty-five out of 60 females in this series were recorded as being pregnant. According to Bailey (1924, p. 528), the gestation period for *Microtus pennsylvanicus* is twenty-one days. A. B. Howell (1924, p. 989) says, "For the first few days after impregnation the embryos are so small as to escape detection by the average collector, who gives but a hasty glance into the abdominal cavity. The writer has no means of knowing the exact time at which appreciable swellings within the uterus indicate clearly that the animal is pregnant, but it is certainly more than three days. If we say three days, to be conservative, then only six out of seven pregnant females are recorded as in this condition by the careful collector." If this proportion holds, then 29 instead of 25 out of 60, or approximately one half of the females, were probably pregnant. Unfortunately the number and size of the embryos were not recorded in all instances. Table 1 gives the number per uterus, size of embryo, and date of capture, for 19 females. In size the embryos range from 3 to 23 mm with an average length of 10.6 mm. The embryos of no. 8336 were recorded as having a length of 35 mm, but this is obviously an error, and was disregarded in determining the mean.

A. B. Howell (1924, p. 989) found that the embryos of *Microtus montanus yosemite* ranged from 2 to 16 mm in length, those of the latter size being at practically full term. The difference which this would indicate between *M. m. montanus* and *M. p. pennsylvanicus* in size of the young at birth is surprising in view of the fact that the adults of the two scarcely differ in size. The discrepancy in recorded embryo size may in part be the result of different methods of measurement.

In one female only a single embryo was found, but this is apparently not a normal condition. Disregarding this individual, the number of embryos per uterus varied from 4 to 8 with an average of 6.05. Howell (1924, p. 989) states that in *Microtus m. yosemite* there were more embryos in the larger than in the smaller females. From the present study there is no indication that this condition exists in *M. p. pennsylvanicus*, for the average number of embryos per uterus for the five largest females, as judged by condylo-basilar length, was 5.8, while the average for the five smallest was 6.4. These figures are, of course, not conclusive. If size is an indication of age, as seems probable, we would expect, from what is known of domestic animals, that the larger animals would be more fecund. Also, Howell (1924, p. 989) reports that there were fewer pregnant females among the larger than among the smaller specimens. This again is not indicated by the present figures.

The external measurements, total length, tail, hind foot, and ear from notch, were taken in the field by Mr. Doutt and Mr. Black. Since such measurements vary considerably with the length of time that the animal has been dead, they are not so accurate as measurements made on the cleaned skulls. Howell (1924, p. 985) says "It is thus seen that even when the measurement is taken carefully by the same person total length varies more than 5 percent, according to the length of time that has elapsed between death and time of measuring. There must be at least 5 percent additional difference in this figure when it is taken by several collectors, making in all a possible error of 10 percent in the total length as given upon the labels of the average study skin."

TABLE 1.—*List of embryos found in nineteen female Microtus, showing number of embryos per uterus, length of embryos, and date on which specimen was taken*

CARNEGIE MUSEUM CATALOGUE NUMBER	NUMBER OF EMBRYOS	LENGTH OF EMBRYOS	DATE OF CAPTURE
		mm.	
7621	6	6	April 8
7967	6	7	" 16
8012	6	9	" 20
8028	6	10	" 21
7652	6	10	" 24
8103	5	3	" 24
8125	1	6	" 26
8136	6	4	" 29
8135	5	23	" 29
8316	7	7	May 6
8228	6	12	" 8
8204	6	22	" 15
7688	8	18	" 17
8316	6	6	" 18
8314	6	17	" 18
8317	6	9	" 18
8328	4	12	" 19
8340	6	10	" 21
8336	7	?	" 22

All measurements are given in millimeters. The mean, standard deviation and coefficient of variability have been calculated for each measurement. Tables 2 and 3 show these figures for the male and female series.

The total length of the specimens was taken in the usual way, from the nose to the tip of the tail vertebrae. In the male series the extremes for this measurement range from 184 to 145, a difference of 39; and in the females from 181 to 140, a difference of 41. The females have a larger coefficient of variability, 14.87% than do the males, 12.49%. This greater variability in the females is not borne out by the cranial measurements, for most of which the males are more variable than the females. It is apparently a reflection of the high degree of variability shown in tail length by the females of this series. The mean total length of the males is 165.35, and of the females is 160.8.

TABLE 2.—*Mean, standard deviation, and coefficient of variation for Microtus pennsylvanicus pennsylvanicus, males*

MEASUREMENT	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
Total length	165.35 ± 1.90	20.65 ± 1.33	12.49 ± .80
Tail	45.65 ± .98	10.75 ± .69	23.55 ± 1.51
Hind foot	20.50 ± .25	2.82 ± .18	13.66 ± .87
Ear from notch	13.94 ± .27	3.02 ± .20	21.66 ± 1.40
Total length of skull	27.21 ± .18	2.01 ± .14	7.35 ± .48
Condylo-alveolar length	17.29 ± .10	1.15 ± .07	6.63 ± .42
Diastema	8.33 ± .07	.78 ± .05	9.36 ± .78
Condylo-basilar length	25.68 ± .18	1.96 ± .13	7.64 ± .49
Incisive foramen	4.84 ± .07	.83 ± .05	17.07 ± 1.09
Molar tooth row	6.46 ± .05	.51 ± .03	7.88 ± .52
Rostral breadth	4.09 ± .04	.39 ± .02	9.63 ± .61
Interorbital breadth	3.71 ± .03	.35 ± .02	9.33 ± .59
Zygomatic breadth	15.04 ± .13	1.39 ± .09	9.22 ± .60
Lambdoidal breadth	12.19 ± .09	.95 ± .06	7.78 ± .50
Height of skull	8.95 ± .07	.76 ± .05	8.44 ± .54
Condylo-zygomatic length	21.22 ± .16	1.75 ± .11	8.25 ± .53
Alveolar width	5.20 ± .03	.35 ± .02	6.65 ± .42
Cranial capacity (No. 10 shot)	116.98 ± 1.90	17.05 ± 1.24	14.57 ± 1.13

TABLE 3.—*Mean, standard deviation, and coefficient of variation for Microtus pennsylvanicus pennsylvanicus, females*

MEASUREMENT	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION
Total length	160.80 ± 2.44	23.95 ± 1.72	14.87 ± 2.0
Tail	42.89 ± 1.12	11.04 ± .79	25.74 ± 1.98
Hind foot	20.12 ± .25	2.34 ± .18	11.63 ± .85
Ear from notch	13.56 ± .30	2.89 ± .22	21.31 ± 1.59
Total length of skull	26.65 ± .18	1.81 ± .13	6.80 ± .47
Condylo-alveolar length	17.04 ± .12	1.13 ± .08	6.62 ± .46
Diastema	8.19 ± .08	.83 ± .06	10.11 ± .70
Condylo-basilar length	25.16 ± .18	1.89 ± .13	7.51 ± .51
Incisive foramen	4.64 ± .07	.68 ± .05	14.60 ± 1.01
Molar tooth row	6.42 ± .04	.45 ± .03	6.99 ± .48
Rostral breadth	4.06 ± .03	.36 ± .02	8.84 ± .61
Interorbital breadth	3.68 ± .03	.33 ± .02	8.99 ± .62
Zygomatic breadth	14.78 ± .12	1.18 ± .08	8.05 ± .58
Lambdoidal breadth	11.96 ± .08	.86 ± .06	7.21 ± .50
Height of skull	8.82 ± .07	.72 ± .05	8.16 ± .57
Condylo-zygomatic length	20.88 ± .18	1.90 ± .13	9.09 ± .63
Alveolar width	5.22 ± .04	.45 ± .03	8.62 ± .60
Cranial capacity (No. 10 shot)	113.70 ± 1.82	16.60 ± 1.28	14.50 ± 1.13

Length of tail is an unreliable measurement. Not only does it vary with the length of time that the animal has been dead, but also, the tip is probably often injured in the wild state, so that the measurement given may not be indicative of

the normal length of the tail. It is the most variable measurement in the whole series. The extremes for the males are 58 and 35, with a difference of 23. In the female series they range from 52 to 35, a difference of 17. However, as in the last measurement, the females show a greater degree of variability. The coefficient of variability for the males is 23.55% and for the females 25.74%. The mean for the male series is 45.65, for the female, 42.89. The measurement shows little correlation with other measurements.

The length of hind foot is the least variable of the external measurements, although more variable than most of the skull measurements. The males vary from 22 to 18, a difference of 4, and the females also from 22 to 18. The mean for the males is 20.50, and for the females 20.12. The difference is so slight as to be of little significance. The coefficient of variability is 13.66% in the males, and 11.63% in the females. This greater degree of variability in the males agrees with Howell's findings in *yosemite* and is in accord with the differences found in the skull measurements. Length of hind foot shows little correlation with age as indicated by size of skull.

Ear length is, next to tail length, the most variable of the measurements. It is rather difficult to take accurately, and like the other external measurements, varies with the length of time the animal has been dead. In both male and female series the extremes range from 16 to 12, a difference of 4. In the males the mean is 13.94, and in the females, 13.56, scarcely a significant difference. The coefficient of variability is 21.66% for the males, and 21.31% for the females. This measurement appears to be slightly better correlated with length of skull than are the length of hind foot and length of tail.

It is apparent that the external measurements are extremely variable. While some of this variation is doubtless due to the difficulties in measuring mentioned above, there is little doubt that the skull measurements are in fact less variable.

The skull measurements were taken with vernier calipers and have all been repeated at least twice.

Total length of skull was taken from the condyles to the most anterior point of the incisors. The longest skull in the male series measures 28.6, the shortest 25.4, a difference of 3.2. The longest female skull is 28.7, the shortest 25.4, a difference of 3.3. The mean total length for the females is smaller however, than that for the males, 26.65 for the females as opposed to 27.21 for the males. The measurement in both groups is one of the least variable of the whole series, 7.35% in the males and 6.80% in the females. This difference in the coefficient of variability in the two sexes is too slight to be of any statistical significance, but when the whole series of measurements is regarded the fact that the males consistently show a slightly higher degree of variability is perhaps not without meaning.

The condylo-alveolar length was measured from the anterior margins of the molar alveoli to the occipital condyles. It is the most constant measurement in the entire series, with coefficients of variability of 6.63% in the males and 6.62% in the females. In the males, the extremes vary from 18.4 to 16.3, a difference of 2.1, and in the females from 18.2 to 16.2, a difference of 2.0. Here again the

mean length of the female series is smaller, 17.29 in the males as opposed to 17.04 in the females.

The length of the diastema was taken between the anterior margins of the molar alveoli and the posterior margins of the incisive alveoli. For the male series it ranges from 9.1 to 7.6, a difference of 1.5. In the females the extremes are 9.0 and 7.5, a difference of 1.5. The mean for the male series is 8.33, for the female, 8.19. The measurement is rather variable, 9.36% in the males and 10.11% in the females. This measurement is one of the three skull measurements for which the females show a greater degree of variability than do the males. These figures indicate that most of the variability in the length of the skull is due to differences in the rostrum rather than in the cranium.

The condylo-basilar length was determined by adding the condylo-alveolar length and the diastema. It is more variable than the former, but less so than the latter, 7.64% in the males and 7.51% in the females. In the males it ranges from 27.1 to 23.9, with a difference of 3.2; in the females from 27.2 to 23.9, a difference of 3.3. It is interesting to note that the two measurements forming the condylo-basilar length do not always vary together. In skull no. 7619, which has a condylo-basilar length of 25.9, the condylo-alveolar length is 17.3 and the length of the diastema is 8.6, while in the case of skull no. 7937, with the same condylo-basilar length, the condylo-alveolar length is 17.8 and the diastema is 8.1. Length of cranium therefore does not always vary directly with length of rostrum, although this is usually the case.

The length of the incisive foramen was taken on the right side of the skull. In some instances there is a difference of one or two millimeters between the sides of the same skull. It is an exceedingly variable measurement, 17.07% in the males, and 14.60% in the females. The extremes for the male series are 5.6 and 4.2, a difference of 1.4. The females range from 5.6 to 4.1, a difference of 1.5. This measurement is the most variable of all the skull measurements, and shows little correlation with the size of the skull. The mean for the male series is 4.84, that for the female series is 4.64. The males are 2.47% more variable.

The length of the molar tooth row was taken from the anterior to the posterior edge of the molar alveolus on the right side of the skull. It is a rather difficult measurement to take accurately in instances where the molars are loose or perhaps missing. One of the male skulls was slightly broken, so that only 55 are represented in the measurements for this character. It varies in the case of the males from 7.0 to 5.9, a difference of 1.1, and in the females from 7.0 to 6.0, a difference of 1.0. It shows very little correlation with the total length of the skull. The means for the two series are very close, 6.46 in the males and 6.42 in the females. The measurement is not very variable, 7.88% in the males, and 6.99% in the females. Howell (1924, p. 1010) found the females in his series to be slightly more variable in respect to this character than the males, but this is not the case in the present study, where, as usual, the males are somewhat more variable.

The rostral breadth was taken across the rostrum directly anterior to the antorbital fossae. In the male series it ranges from 4.5 to 3.7, a difference of

0.8, and in the females from 4.4 to 3.8, a difference of 0.6. The difference between the mean for the males, 4.09, and that for the females, 4.06, is too slight to be of any significance. The coefficient of variation is fairly large, 9.63% in the males and 8.84% in the females. The measurement does not show much correlation with the length of the skull.

The interorbital breadth was taken across the narrowest part of the interorbital constriction. This region is not much constricted in *Microtus*, being but slightly smaller than the rostral breadth. The extremes for the male series are 4.0 and 3.4, a difference of 0.6. For the females they are 4.1 and 3.3, a difference of 0.8. The mean for the male series is larger, being 3.71, while that for the female series is 3.68. This difference, however, is scarcely significant. The measurement is quite variable, 9.33% in the males and 8.99% in the females. Here again the sexual difference has little meaning. There is not much correlation between the interorbital breadth and the length of skull, nor is there as much as one might expect between the rostral and interorbital measurements. In skull no. 8235, the former is 4.5 and the latter 3.6, while in skull no. 7709 they are 4.0 and 3.9 respectively. These are rather exceptional cases.

The zygomatic breadth is the greatest distance across the zygomatic arches. Although these arches are fairly broad and strong in *Microtus* they are sometimes broken in cleaning, so that some of the skulls, otherwise perfect, lack the jugal bones and are not included in this series of measurements. The figures represent 53 males and 44 females. In the male series, the extremes range from 16.3 to 13.6, a difference of 2.7, and in the females from 16.2 to 13.6, a difference of 2.6. The mean for the male series is 15.04, for the female series, 14.78. The coefficient of variability in the males is 9.22%; in the females, 8.05%. This measurement is better correlated with the length of skull than are the other measurements for width.

The lambdoidal breadth was taken across the lambdoidal crests. In one male skull the crest was slightly crushed so that only 55 are included in the figures. The males vary from 13.2 to 11.2, a difference of 2.0. The females range from 12.9 to 11.4, a difference of 1.5. The mean for the male series is 12.19; for the female, 11.96. The measurement is the least variable of those for width, 7.78% in the males and 7.21% in the females. The sexual difference has little significance. Like the zygomatic breadth, this measurement is fairly well correlated with the length of skull.

Height of skull was measured as a line from the highest part of the center of the roof of the cranium passing vertically to a line drawn along the center of the palate. It was felt that a plane passing along the highest points of the molar teeth, such as was used by Howell (1924, p. 998) is too apt to be affected by whether the teeth are loose in the sockets, and that therefore a line along the center of the palate gave a more accurate measurement. In two skulls the parietal bones were loosened so that the measurements include 55 males and 47 females. In the males, the measurements range from 9.0 to 7.5, a difference of 1.5, and in the females, from 9.1 to 7.6, also a difference of 1.5. In the males the mean is 8.95; in the females, 8.82. The coefficients of variability are 8.44% in the males and

8.16% in the females. These differences are not great enough to be of much significance. The measurement is fairly well correlated with the measurements for length, less well so with those for width.

The condylo-zygomatic length was taken on the right side of the skull from the occipital condyle to the anterosuperior edge of the zygomatic branch of the maxilla. In the male series the extremes range from 22.6 to 19.9, a difference of 2.7, and in the females from 22.7 to 19.9, a difference of 2.8. The means for the two series are, respectively, 21.22 and 20.88. The coefficient of variation is, for the males, 8.25%, and for the females, 9.09%. This measurement and the following one, with the diastema, are the only ones in the whole series in which the females are more variable than the males, and even here the difference is so slight as to be of little significance.

The alveolar width is the greatest distance between the lateral borders of the molar tooth rows. The measurement is apt to be affected by the looseness of the molars and is therefore not so reliable as some of the others. The extremes in the male series are 5.6 and 4.8, a difference of 0.8; in the females the extremes range from 5.8 to 4.9, a difference of 0.9. The mean for the male series is 5.20, for the female, 5.22. This measurement is the only one for which the mean for the females exceeds that for the males, and even here the difference is so slight as to be of no significance. The females are also more variable than the males, the coefficient of variation for the latter being 6.65%, and for the former, 8.62%. It is interesting to note that in the measurements concerned with the molar teeth, that is, the length of the tooth row and the alveolar width, there is less difference in size between the sexes than for most of the other measurements.

It was difficult to find a convenient method for measuring cranial capacity. Small units of measurement, such as dust shot, inclined to slip through the foramina of the skull, and also varied greatly, due to differences in packing, in the number which could be placed in the same skull at different times. Also, such small units were difficult to count, and the final count was found to be open to error. Too large shot tended to minimize the amount of variation. No. 10 shot was finally found to be fairly satisfactory, but the measurement was not entirely accurate. It must be remembered that the size of the cranium is determined by the breadth and height of the skull as well as by its length, although it seems to vary most in accordance with the latter. We should, therefore, expect to find a greater degree of variability for this measurement than for the others of the skull. In the male series, the number of shot that can be placed in a skull ranges from 134 to 96, a difference of 38. In the females the extremes are 130 and 103, a difference of 27. These figures for the females include only 47 skulls, since one skull was slightly broken. The mean for the male series is 116.98, for the females, 113.70. The difference is negligible. The coefficient of variability for the males is 14.57%, for the females, 14.50%. It is, as was anticipated, larger than the variability shown by the other skull measurements with the exception of the length of the incisive foramen.

Although in most of the measurements the sexual difference in size between the two series is so slight as to be negligible when considered for a single measure-

ment, the fact that the males almost consistently average slightly larger may be not without significance when the whole series of measurements is considered. The same statement may be made with regard to the coefficient of variability. In these animals, as in most mammals in which the comparative variability of the sexes has been studied, the female is the more conservative of the two.

Schultz (1926) has published the results of a comparative study of variability in the Platyrrhine monkeys and in man. The average coefficient of variability for cranial measurements in adult male *Alouatta* is given as 3.10%; for *Ateles* it is 4.41%; and for adult male Swiss it is 3.51%. The average coefficient of variation for the skull measurements in the series of *Microtus p. pennsylvanicus* is 8.85%. *Microtus* is thus apparently more variable than is man. Probably the same will be found to be true for many of the smaller mammals when we know more about the range of individual variation in these forms.

TABLE 4.—*Comparison of means for skull measurements of Microtus from Pymatuning Swamp and Beaver County*

MEASUREMENT	MEAN FOR SERIES FROM PYMATUNING SWAMP	MEAN FOR SERIES FROM BEAVER COUNTY
Total length of skull	27.21	26.50
Condylo-alveolar length	17.29	16.82
Diastema	8.33	8.14
Condylo-basilar length	25.68	24.96
Incisive foramen	4.84	4.93
Molar tooth row	6.46	6.40
Rostral breadth	4.09	4.09
Interorbital breadth	3.71	3.83
Zygomatic breadth	15.04	14.83
Lambdoidal breadth	12.19	12.04
Height of skull	8.95	8.21
Condylo-zygomatic length	21.22	20.61
Alveolar width	5.20	5.37

Unfortunately, no comparable series of meadow mice from a different locality was available for comparison. However, 16 specimens, 10 males and 6 females, from Beaver County, Pennsylvania, were measured. Inasmuch as *Microtus p. pennsylvanicus* becomes larger towards the south, we should expect that, if any difference were found between the two series, it would be that the Beaver specimens are slightly larger. Table 4 shows a comparison of the mean measurements for the males from the two localities. For all measurements except the length of incisive foramen, interorbital breadth, alveolar breadth, and rostral breadth, the Pymatuning specimens are larger. For the rostral breadth they are the same. The same results were obtained when the female series were compared. This would seem to indicate that there is a difference in proportion between the two populations. The Beaver specimens seem to be slightly shorter and slightly broader in the fore part of the skull. Needless to say, such results would have to be checked on a much larger series before any definite statement could be

made, but at least these differences suggest interesting possibilities for future study.

The molar teeth were examined for variations in pattern. Such variation is fairly common, especially in the third upper molars. The normal pattern of this tooth consists of an anterior crescent, three closed triangles, and a posterior loop with two inner lobes, making three outer and four inner salient angles (see fig. 1). In this series of specimens, however, the tooth shows a progressive modification by which the posterior loop becomes three-lobed. The gradations by which the series passes from one form to the other are very small, and it is difficult in many cases to say whether the tooth shows the extra lobe. In approximately 20 percent of the skulls the structure is well enough developed to be quite noticeable. It may be present on one side of the jaw and not on the other. Howell (1924, p. 1012) records a similar variation in specimens of *Microtus montanus yosemite*, although it is apparently not so common in his series as in the present one. Miller (1896, p. 64) has also remarked on the occurrence of this variation. The three-lobed condition is normal in *M. chrotorrhinus*. It is interesting to note that a somewhat analogous situation is reported by Shreuder (1933, pp. 20–21) in his study of Microtinae of the Netherlands. *Microtus a. arvalis* has normally four inner salient angles, as has *pennsylvanicus*. In certain cases, only three are present and all gradations between the two conditions are found.

Another variation that sometimes appears in the third upper molar of the Pymatuning series is the presence of a small fourth outer salient angle. This is another feature that is typical of *chrotorrhinus*. Indeed, the presence of both of these characters in a well developed condition would give a tooth similar to a *chrotorrhinus* M^3. Komarek (1932, p. 156) reports a specimen of *chrotorrhinus* that has one angle less than normal.

A possible explanation of these facts is that the third upper molar in *Microtus* is undergoing reduction. The most primitive condition is found in *chrotorrhinus*, in which the extra outer salient angle and extra inner angle are both present normally. In *pennsylvanicus* these two angles have almost disappeared, with the fourth outer angle more nearly gone than the fifth inner angle. Both, however, appear occasionally. A similar condition is found in *montanus*. In the case of *arvalis*, these two angles have completely disappeared and reduction of the fourth inner angle is becoming evident. Unfortunately, not enough is known of the evolution of the teeth of *Microtus* to show whether these deductions are correct. Much more fossil material must become available before any definite statements can be made.

Other variations occur in the teeth, although none are so marked as these. The posterior triangle of the first upper molar may develop a loop at the posterior end. There is a good deal of variation in the shape of the anterior trefoil of the first lower molar. The second molars in both the upper and lower jaws are almost constant. In skull no. 8139, which is apparently fully adult in other respects, the third lower molars have just appeared, and scarcely rise above the level of the bone.

SUMMARY

A study was made of individual variation in a series of the Pennsylvania meadow mouse, *Microtus pennsylvanicus pennsylvanicus* (Ord).

There is little apparent variation in coat color. Molt is not visible on the surface and does not appear to be seasonal in occurrence.

Approximately half of the females were pregnant, with an average of 6 embryos per uterus. The embryos average 10.61 mm in total length.

External measurements are found to be very variable. The most variable is the tail length; the least variable, the length of hind foot.

Skull measurements are less variable than the external measurements. The three least variable measurements are the condylo-alveolar length, the total length of the skull, and the length of the molar tooth row. The three most variable measurements are the length of the incisive foramen, the cranial capacity, and the length of the diastema.

A slight sexual difference is shown between the male and female series, with the males averaging somewhat larger and more variable.

Considerable variation is found in the pattern of the molar teeth. The third upper molar is apparently in a rather active stage of reduction.

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THE BODILY STRENGTH OF CHIMPANZEES

By Glen Finch

Some time ago, Bauman (1923, 1926) reported a few observations on the bodily strength of chimpanzees. His conclusions, based on dynamometer measurements, indicate that the adult chimpanzee is several times as strong as man. The present investigation was undertaken as an attempt to clarify and to supplement Bauman's data.

Eight chimpanzees from the Yale Laboratories of Primate Biology colony were used as subjects (all four of the adult males in the colony and four adult females). Of these, five are among the healthiest and most vigorous animals in the colony; the other three (Jack, Cuba, and Pati) cannot be characterized as especially vigorous and healthy, although all were in good condition at the time of the present experimentation.

The technique utilized consisted of the subjects' pulling in an incentive placed on a small carriage which was attached to a 1-inch Manila rope, resistance being furnished by a variable weighting of the rope. Figure 1 is a profile diagram of the apparatus. It will be noted that, from the weights, a rope is led over a pulley system so arranged that the animal is required to pull with a power twice as great as the weights (*i.e.*, a unit movement of the rope results in 2 units of movement of the weights). It will also be noted that a ratchet (attached to the first pulley above the weights) was provided, which prevented backward movement; the ratchet engaged with every 3 inches of forward movement of the incentive. The weights used were discs of cast iron, each weighing 10 pounds.

With such a system as that diagrammed (fig. 1), it is obvious that the force a subject must apply to move the incentive is determined by (1) the gravitational resistance of the load, (2) the inertia of the system, (3) the power of the pulley system, and (4) the frictional resistance of the system. In order to translate the subjects' pulls into absolute terms, the force necessary to move the system at each of the 10 pound weight increments was determined by attaching a spring-scale to the rope in the subject's position and pulling it with a windlass. Scale-readings were taken at the instant the system was put in motion. Figure 2 presents the calibration data. Each of the points represents the mean of 5 scale readings. The straight-line, fitted to the data graphically, was drawn so that the force of pulls beyond the scale's calibration (*viz.*, beyond 300 pounds) might be estimated.

Each subject was tested with a modified "method of limits" technique. Preliminarily, the subjects were accustomed to the apparatus through several days with increasingly greater resistances to their pulls, each subject being allowed to recover the incentive (a small piece of fruit) with each completed pull (a completed pull consisted of pulling in the rope a distance of 9 to 12 inches). Test trials were given in two days' sessions, the first day with normal prior food-deprivation (each subject was tested in the morning before a major feeding), the second day with 24 hours prior food-deprivation.

Tests were conducted as follows: With one small piece of banana as incentive, the subject was given the rope and allowed to pull against the maximal resistance that he had previously overcome. When the incentive was recovered, the rope was withdrawn, one 10 pound weight was added to the load, another piece of banana was provided as incentive, the subject was given the rope and allowed to pull. If the subject failed to move the system in one minute, an additional piece of fruit (apple, orange, or banana) was added to the incentive, and so on with further additions of fruit each minute until ten minutes had elapsed, at which time the test was terminated and the subject's maximal pull was recorded as the resistance which he had overcome (as judged by a movement of the incentive of at least 3 inches). It might be noted that the size of the incentive became comparatively very great before a trial was recorded as failure. Addi-

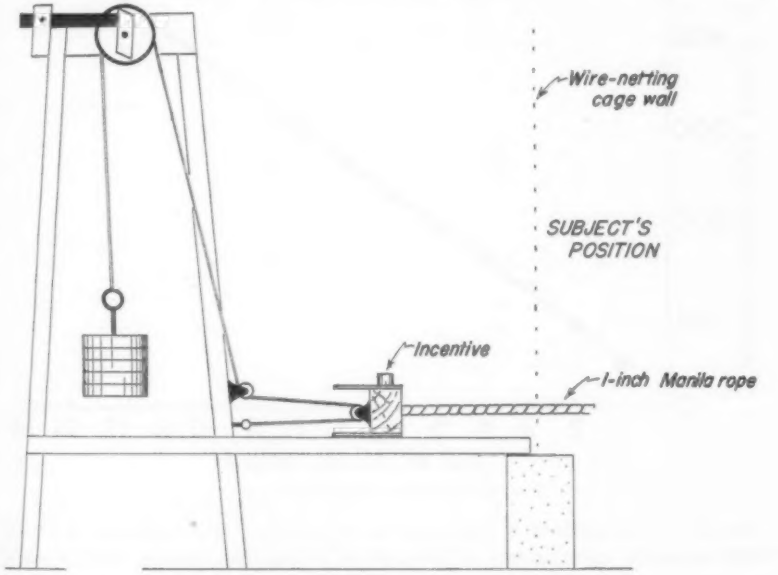

FIG. 1. Diagram of strength-measuring apparatus

tional 10 pound weights were added, one at a time, until the subject failed to move the system in ten minutes.

In order to provide comparative human data, four members (adult males) of the staff of the Yale Laboratories consented to serve as subjects. They were tested in the same way as the chimpanzees (except that social incentives were substituted for food motivation and the subjects were tested in only one day's session).

Table 1 presents the bodily weight, maximal pulls, and ratio of maximal pulls/bodily weight for all subjects. From this table, it will be seen that the heaviest

chimpanzee (Jack) was considerably (13 pounds) lighter than the lightest human subject. Under normal hunger conditions, the male chimpanzees greatly outpulled the females (males' pulls range from 375 to 487 pounds, females' from 227 to 300). Comparison of the pulls after the 24-hour food-deprivation is difficult because of the failure of two animals (Bokar and Cuba) to pull. Only three animals (Pan, Lita, and Cuba) bettered their pulls with increased hunger. The human pulls range from 338 to 525 pounds. One of the human subjects (number 1) outpulled all the chimpanzees, and all the human subjects outpulled all the female chimpanzees.

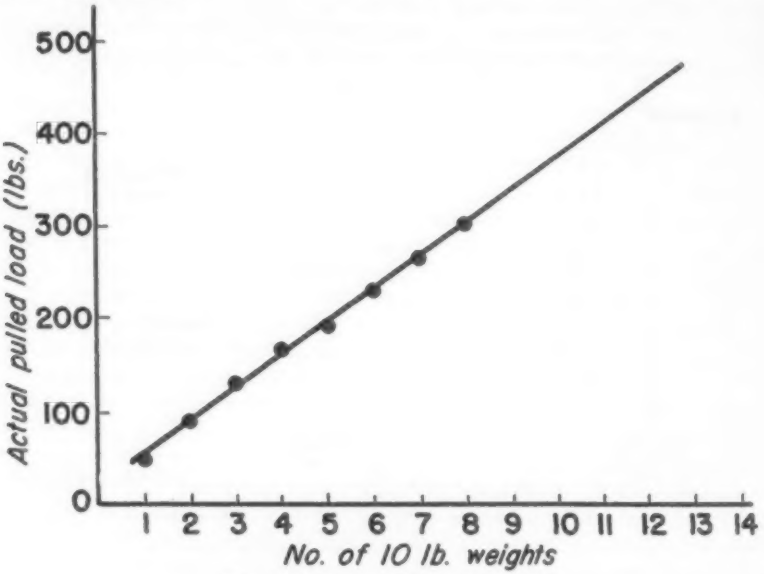

FIG. 2. Apparatus calibration curve

Statistical comparison of the records, especially the computing of bodily weight-strength correlations, is difficult or impossible because of the small number of subjects. It seems reasonable to conclude, however, that there is no great *absolute* strength discrepancy between the human and chimpanzee males and that the males of both species are absolutely stronger than the female chimpanzees. It seems strongly indicated that the male chimpanzees, pound for pound of bodily weight, are relatively stronger than either the human males or the chimpanzee females.

All the chimpanzee subjects impressed human observers as exerting maximal or near-maximal effort on their maximal pulls. The human subjects testified that their pulls were maximal.

Reconciliation of the present data with that presented by Bauman is difficult.

Differences in technique hardly seem adequate to account for the great differences in results. Examining Bauman's data critically, we find that his conclusions are based largely upon a trial of three, or possibly of four, pulls registered by two animals. The adult female chimpanzee, Suzette (estimated weight, 135 pounds), *in a rage*, registered one pull of 1260 pounds; she also registered, *deliberately*, a pull of 905 pounds. The adult male, Boma (estimated weight 165 pounds), registered one-hand pulls of 847 and 640 pounds. The only other animal that Bauman could induce to pull (the adult female chimpanzee, Johanna) registered a pull of 378 pounds. Suzette's phenomenal pull might be attributed to the fact that she was enraged when pulling, whereas none of the present

TABLE 1

SUBJECTS	BODILY WEIGHT	MAXIMAL PULL		RATIO OF MAXIMAL PULL/BODILY WEIGHT	
		Normal	24-hour hunger	Normal	24-hour hunger
	lbs.	*lbs.*	*lbs.*		
Male chimpanzees					
Bokar	107	487	*	4.6	—
Jack	122	450	450	3.7	3.7
Frank	108	450	413	4.2	3.8
Pan	106	375	413	3.5	3.9
Female chimpanzees					
Lita	103	300	375	2.9	3.6
Cuba	82	300	*	3.7	—
Mimi	109	227	264	2.1	2.4
Pati	103	227	194	2.2	1.9
Human males					
1	190	525		2.8	
2	145	487		3.4	
3	145	450		3.1	
4	135	338		2.5	

* Refused to pull any weight.

subjects were greatly emotionally disturbed, although usually obviously highly motivated; but still, her deliberate pull of 905 pounds, made when *not* enraged, greatly exceeds the highest pull recorded in the present experiment. The results of Bauman's tests of seven college football players are closely comparable to the present human tests (Bauman's range—327 to 460 pounds; present human pulls range from 338 to 525 pounds). Inasmuch as Bauman states that the same apparatus was used in testing his chimpanzee and human subjects, the discrepancies can hardly be attributed either to apparatus differences (unless Bauman's apparatus-calibration changed during the interval between chimpanzee and human tests), nor to the bodily weight superiority of Bauman's chimpanzee subjects.

CONCLUSIONS

1. Chimpanzees were taught to pull in a rope against resistance to procure a food incentive. Four male chimpanzees, tested under normal hunger conditions, registered maximal pulls of 375, 450, 450, and 487 pounds; under the same conditions, four female chimpanzees' pulls were 227, 227, 300, and 300 pounds.

2. Prior food-deprivation of 24 hours resulted in two animals' refusing to pull; three bettered their "normal" records; one pulled the same under both conditions; two pulled less.

3. Four adult male human subjects, tested under comparable conditions (with social incentives), pulled 338, 450, 487, and 525 pounds.

4. These results seem to indicate: (a) Adult human males and adult chimpanzee males are roughly equal in absolute pulling strength, (b) chimpanzee females are inferior in pulling strength to human and chimpanzee males, and (c) pound for pound of bodily weight, chimpanzee males are superior in pulling strength to human males and to chimpanzee females.

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TWO NEW RACES OF THE PUMA

BY E. A. GOLDMAN

The pumas of the northern part of the Rocky Mountain region have hitherto been assigned to *Felis concolor hippolestes* of Wyoming. Distinctive cranial details, however, seem to warrant the recognition of a separate race. In marked contrast, toward the southern end of the range of the species, are specimens from Descalvados and Corumbá, Brazil, and from Puerto Suarez, extreme eastern Bolivia, referred by Nelson and Goldman (Jour. Mamm., vol. 10, no. 4, p. 345, 1929) to *Felis concolor osgoodi*, and which have also been subjected to revision. A few additional specimens have been examined, and more familiarity with the group has convinced me that the pumas of the lowlands of Matto Grosso, characterized by very light rufescent coloration and slender skull, can not satisfactorily be identified with any of the neighboring geographic or ecologic races. For two of the specimens from Descalvados, Brazil, one of which is here designated as the type of a new subspecies, I am indebted to Alfred M. Bailey, Colorado Museum of Natural History, who has generously donated them to the National Museum collection. My thanks are also due to C. C. Sanborn, Field Museum of Natural History, and H. E. Anthony, American Museum of Natural

History, for the loan of specimens used for comparison. The new subspecies are described as follows:

Felis concolor missoulensis, subsp. nov.

Northern Rocky Mountain Puma

Type specimen.—Adult male, skin and skull, no. 262116, U. S. National Museum (Biological Surveys collection); from Sleeman Creek, about 10 miles southwest of Missoula, Missoula County, Montana; collected December 30, 1936, by Ronald and Carrol Thompson; X-catalog number 27706.

Distribution.—Northern Rocky Mountain region from Yellowstone National Park, Wyoming, north to Jasper Park, Alberta, and the Peace River District, British Columbia; east to western Saskatchewan and northwestern North Dakota. Intergrades on the west with *Felis concolor oregonensis* and on the south with *Felis concolor hippolestes*.

General characters.—Size large; color rather pale; skull large and massive, but relatively short and rounded, with widely spreading zygomata. Differs from *hippolestes* of central western Wyoming in cranial details, especially general shortness, and wider spread of zygomata. Differs from *oregonensis*, of the Cascade Range, Washington, in paler color as well as in cranial details.

Color.—Type: Top of head, neck, and narrow median dorsal area near "tawny" (Ridgway, 1912), slightly darkened by black-tipped hairs; over the same parts an admixture of white hairs is too sparse to affect materially the general tone; tawny of narrow median dorsal area giving way rather abruptly to light "cinnamon", paling gradually along sides and outer surfaces of limbs to near "pinkish buff" on feet; upper lips (except blackish spots at base of vibrissae), chin, and throat, pure white; under surface of neck pale buff, or between "pinkish buff" and "pale pinkish buff"; chest, inner sides of limbs, and under parts white, the "drab-gray" under color showing through; middle of face a grayish brown mixture; supraorbital spots white, as usual in the group; ears blackish externally, becoming grayish near edges, covered internally with longer white hairs; hairs around pads on soles of feet blackish; tail above similar to back, but less distinctly "tawny", more mixed with black to near tip, which is black for about two inches, becoming brownish buffy below. In a skin from 18 miles southeast of Hamilton, Montana, the median dorsal area is more vivid and near "orange-cinnamon" in tone.

Skull.—Similar in general size to that of *hippolestes*, but shorter, broader, and somewhat flatter; zygomata more widely spreading; rostrum and palate distinctly shorter; vestigial upper premolars set in a narrower space behind canines; diastema behind lower canines shorter; dentition about the same. Compared with that of *oregonensis* the skull is similar in general size but is shorter, broader, and flatter; zygomata more widely spreading; frontal region less elevated; rostrum and palate usually shorter, but vestigial upper premolars set in a gap of similar extent; diastema in lower jaw shorter; dentition usually lighter.

Measurements.—No external measurements available. *Skull:* Type and an adult female from Crow's Nest Pass, Kootenay District, British Columbia, respectively: Greatest length, 221.8; 190; condylobasal length, 203.5, 175; zygomatic breadth, 164.3; 139; height of cranium, 81.5, 70; interorbital constriction, 45.4, 41.6; postorbital processes, 78.7, 76.6; width of nasals (at anterior tips of frontals) 18.5, 15.9; width of palate (across interpterygoid fossa), 28.6, 31; maxillary tooth row, alveolar length (front of canine to back of carnassial), 65.7, 53.9; upper carnassial, crown length, 27.2, 20.7, crown width, 12.5, 10.7; lower carnassial, crown length, 17.7, 15.7; upper canine, alveolar diameter (anteroposterior), 16.8, 11.5.

Remarks.—The range of *missoulensis* along the Rocky Mountains in Alberta and British Columbia, marks the northern limit of the distribution area of the group. On the south, in northern Wyoming, *missoulensis* passes rather abruptly into *hippolestes*, which differs most obviously in the relatively narrower, more elongated skull. Between the Rocky Mountains and the Cascade Range *missoulensis* intergrades with *oregonensis*.

Specimens examined.—Total number, 52, all from the northern Rocky Mountain region.

Felis concolor acrocodia, subsp. nov.

Matto Grosso Puma

Type specimen.—Adult male, skull only; no. 273256, U. S. National Museum (Biological Surveys collection), formerly No. 2390, Colorado Museum of Natural History; from Descalvados, Matto Grosso, Brazil; collected November 25, 1925 by Frederick W. Miller.

Distribution.—Lowlands of the upper part of the Paraguay River Valley, in southwestern Brazil, and eastern Bolivia.

General characters.—Size medium; dorsum nearly clear "tawny" or light "cinnamon rufous", with little or no blackish admixture; skull slender, with frontal region narrow, but highly arched behind postorbital processes; jugal reaching transverse plane of anterior wall of glenoid fossa. Similar in size to *Felis concolor concolor*, of the São Paulo region, Brazil, but differs in cranial details, especially the narrowness of the braincase and frontal region, and less deeply V-shaped nasals. Also similar in size to *Felis concolor osgoodi*, of the mountains of central Bolivia, but ground color of upper parts lighter "tawny", and the median dorsal area lacking the overlying black present in the latter race; frontal region, narrower, more highly arched, and other cranial details different. Differs from *Felis concolor borbensis*, of the Rio Madeira region in lighter, less rich rufescent coloration and in cranial characters.

Color.—(Skin no. 273257, U. S. National Museum, formerly no. 4618, Colorado Museum of Natural History, from Descalvados, Matto Grosso, Brazil): Top of head, neck and median dorsal area to base of tail light rusty reddish, near "tawny", or light "cinnamon-rufous", becoming "cinnamon-buff" on sides of neck, shoulders, along flanks and on outer surfaces of limbs, paling gradually to near "pinkish buff" on feet; lips (except blackish spots near vibrissae), chin, and throat, white; under surface of neck suffused with "pinkish buff"; chest, inner sides of limbs, and inguinal region dull white; belly suffused along sides with "pinkish buff", becoming whitish along median line; face in general light buffy, with a light brownish admixture, the whitish supraorbital spots distinct; ears brownish or blackish externally, thinly clothed internally with whitish hairs; hairs around pads on feet light brownish; tail above similar to back, but thinly mixed along median line with black, below pinkish buff to near tip, which is broken off. Another paratype (no. 28334, Field Museum of Natural History) is similar, and the complete tail is dark brown, near "verona brown", for about one and one-half inches at tip.

Skull.—Skull slender; remarkable for narrowness and height of frontal region, and narrowness of braincase. Similar in size and general form to that of typical *concolor*, but frontal region narrower, more highly arched behind postorbital processes; braincase narrower; nasals less decurved along inner borders and less deeply and broadly V-shaped to form a median trough anteriorly, more pointed posteriorly; frontal pit at posterior ends of nasals deeper—unusually deep for a South American race; coronoid process of mandible higher; auditory bullae larger, more fully inflated; dentition about the same. About the size of that of *osgoodi*, but frontal region narrower, more highly arched; postorbital processes shorter; dentition about the same. About equal in general size, and in narrowness of braincase to *borbensis*, but frontal region more elevated behind postorbital processes; nasals more acutely pointed posteriorly; auditory bullae larger, more inflated; dentition similar.

Measurements.—No body measurements available. *Skull:* Type and a young adult female paratype, respectively: Greatest length, 201.5, 172; condylobasal length, 175.5, 156.4; zygomatic breadth, 135.5, 115.5; height of cranium, 72.8, 60; interorbital constriction, 37.2, 32.4; postorbital processes, 65.9, 57.9; width of nasals (at anterior tips of frontals, 15.7, 15.1; width of palate (across interpterygoid fossa), 28.5, 26.5; maxillary tooth row, alveolar length (front of canine to back of carnassial), 57.5, 53.7; upper carnassial crown length, 22.9, 21.4, width, 11.9, 11.1; lower carnassial, crown length, 17.6, 16.2; upper canine, alveolar diameter (antero-posterior), 14, 10.9.

Remarks.—In the narrowness of the braincase, *acrocodia* suggests relationship to *borbensis*, of the Rio Madeira region, and intergradation across low intervening watersheds seems

probable. Toward the west the Matto Grosso animal doubtless passes into *osgoodi*, and toward the east into typical *concolor*.

Specimens examined.—Total number, 8, all from the Matto Grosso region of southwestern Brazil and eastern Bolivia.

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A POPULATION STUDY OF THE BEECHEY GROUND SQUIRREL IN CENTRAL CALIFORNIA

By F. C. Evans and R. Holdenried

Recent natural history studies have increasingly emphasized the careful quantitative measurement of populations. This logical development from the earlier qualitative description of life histories and habits has been made possible by the improvement of census techniques as well as by the progress of bio-mathematical thought. Our paper deals with a population of a common and economically important species, the Beechey or California ground squirrel, *Citellus beecheyi* (Richardson). This squirrel is the chief rodent pest of California, destroying annually many thousands of dollars worth of crops and serving as a reservoir for diseases, notably plague and tularemia; in 1941 an estimated $400,000 was spent for its control within that state. It is surprising, therefore, that accurate knowledge of this species is lacking in many details. Its taxonomy has recently been revised by Howell (1938), but the only comprehensive report of its natural history is that by Grinnell and Dixon (1918), compiled in part from field experience but largely supplemented with information from scattered sources. The present study of the subspecies *beecheyi* yielded some life-history material, which has been included in this paper, but its main emphasis was upon population dynamics.

The role of ground squirrels in the epidemiology of sylvatic plague has been the subject of comprehensive inquiry in recent years by the George Williams Hooper Foundation for Medical Research. In 1940 it established a field station for ground squirrel study at the Calaveras Reservoir, Alameda County, California (fig. 1). The reservoir, completed in 1925, is the property of the San Francisco Water Department and serves that city as an auxiliary source of supply; it is situated in the Livermore Hills, about 10 miles south of Sunol. The particular area selected for field work adjoined the north and northeast margins of the reservoir on the Alameda-Santa Clara county line. Field work included the trapping, marking, and releasing of ground squirrels for future captures and observations of habits and behavior. A preliminary report on the results of the 1940 season has already been published (Evans and Holdenried, 1941).

In the entire study 1,154 squirrels were caught, of which 949 were marked and released for further observation (Table 1). In 1940 the station was used from April 11 to December 13, with trapping on 157 days and a total of 10,326 trap-days (1 trap set for 1 day = 1 trap-day). In this period 542 squirrels were caught; 433 were marked and released and 109 were removed for laboratory

experiments. In 1941, work extended from April 14 to November 20, with trapping on 96 days and a total of 6,085 trap-days. In this season 545 squirrels were caught; 132 were recoveries from 1940, 329 others were marked and released and the remaining 84 were removed. In 1942, less extensive operations ran from March 31 to July 31, with trapping on 58 days and a total of 3,011 trap-days. The 1942 records include 286 squirrels: 29 recoveries from 1940, 58 from 1941, 187 newly marked and released, and 12 removed.

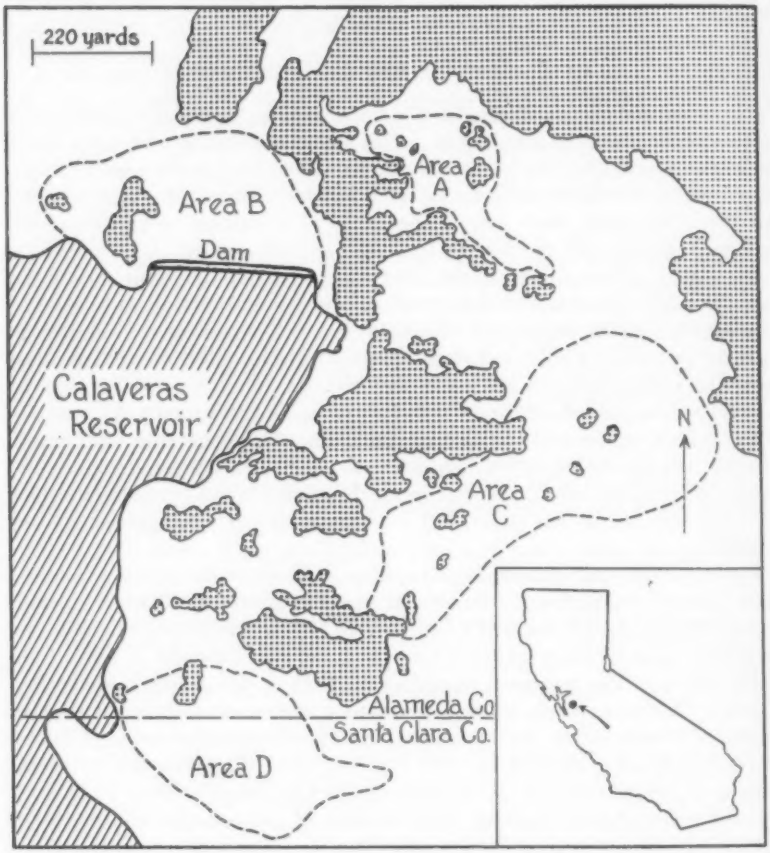

FIG. 1. Maps showing locations of Calaveras Reservoir and of principal trapping areas.

This study was carried out under the auspices of the Hooper Foundation, with the advice and guidance of the Director, K. F. Meyer; it was supported by grants from the Rosenberg and Columbia Foundations. The San Francisco Water Department gave us permission to work on its property and made available to us the weather records from Calaveras Dam. W. C. Jacobsen, Chief of the Bureau of Rodent and Weed Control, California Department of Agriculture,

and G. B. Laing and L. R. Cody, Agricultural Commissioners of Alameda and Santa Clara counties, respectively, gave valuable assistance and cooperation. E. T. Ross, Chief of the Bureau of Sanitary Inspections, California Department of Public Health, assisted with the plague survey made in 1942. Much of the

PLATE 1

Panorama of dam and environs at Calaveras Reservoir

PLATE 2

The trapping areas at Calaveras Reservoir. Upper left, Area A; upper right, Area B; lower left, Area C; lower right, Area D.

continuity of the field work was made possible with the help of A. L. Burroughs, L. H. Fisher, A. S. Loukashkin, R. Rudd, K. E. Stager, and W. M. Thorning. Miss E. Crum of the University of California Herbarium identified the species of plants collected. Opportunity for the senior author to complete the prepara-

tion of the material for publication was provided by the Division of Zoology, College of Agriculture, University of California, where he is now stationed. Barbara D. Blanchard, J. T. Emlen, Jr., and T. I. Storer read and criticized the manuscript. The drawings and maps were done by Emily P. Thompson. We gratefully acknowledge our thanks to all of these, as well as to many others whose interest gave us much encouragement.

THE ENVIRONMENT

Geographically and geologically this area is part of the Mt. Diablo Range. The reservoir covers 1,450 acres and has filled most of the level portion of the Calaveras Valley; its surface is about 740 feet above sea-level. Below the earthen dam at the northern end, Calaveras Creek flows through a deep canyon to Alameda Creek. The hills seldom rise more than 2,000 feet above sea-level, but their slopes are steep, often 20 percent. The southern and western slopes are covered mainly by a fairly dense growth of herbs and grasses that dry up and turn brown in summer. On the northern and eastern slopes, however, and in some deeper ravines with southern exposures, trees and brush form heavy covers; these frequently end abruptly where the herbaceous growth begins (Plate 1).

The area adjoining the reservoir is in the Upper Sonoran life-zone (Hall and Grinnell, 1919; Grinnell, 1935), but some Transition zone species are present, such as the big-leaf maple (*Acer macrophyllum*), black oak (*Quercus kelloggii*), and western gray squirrel (*Sciurus griseus*), and also some Lower Sonoran species, like the yellow-billed magpie (*Pica nuttallii*).

The climate is somewhat arid, but conditions are influenced by the moderate weather prevailing on the coast. Occasionally temperatures exceed 100°F. in summer and drop below 32°F. in winter. Rainfall is largely limited to December, January, February and March, with infrequent showers as early as September and as late as May. In 1940 and 1941 the total rainfall at the reservoir was 30.32 and 25.09 inches, respectively.

The commonest tree is the valley oak (*Quercus lobata*). The coast live oak (*Q. agrifolia*) and blue oak (*Q. douglasii*) occur in small groves and as scattered individuals. Other local trees are willows (*Salix* sp.), big-leaf maple (*Acer macrophyllum*), California laurel (*Umbellularia californica*) and buckeye (*Aesculus californicus*). The brush species include California sagebrush (*Artemisia californica*), coyote brush (*Baccharis pilularis*), poison oak (*Rhus diversiloba*), and blue elderberry (*Sambucus glauca*). Coffee berry (*Rhamnus californica*) and toyon (*Photinia arbutifolia*) help to form local thickets.

Ground squirrels were rarely if ever seen in areas of heavy tree and brush growth, or on ungrazed lands where dense stands of such grasses as *Avena barbata* reached a height of several feet. They were largely restricted to open grasslands supporting relatively short herbaceous growth. Most of these last were heavily grazed by cattle and mule deer (*Odocoileus hemionus*), which kept the plants closely cropped in spite of conditions favorable to rank growth. The grazed areas bore a large variety of plants; many of these grew only during the wet winter and spring and died down after seed production at the beginning of sum-

mer, but a few such, as *Hemizonia*, remained green throughout the dry season. The principal herbaceous species are listed here; those eaten by squirrels (found in cheek pouches or feces, or actually observed) are marked with one asterisk and those eaten most commonly, with two.

****Bromus rubens*
****Bromus mollis*
****Bromus rigidus*
****Festuca megalura*
****Festuca dertonensis*
****Hordeum murinum*
****Avena barbata*
***Chlorogalum pomeridianum*
Allium serratum
***Brodiaea laxa*
Brodiaea capitata
***Glinus lotoides*
***Silene gallica*
***Ranunculus californicus*
***Eschscholtzia californica*
***Sisymbrium officinale*
Tropidocarpum gracile
****Medicago hispida*
****Medicago apiculata*
****Melilotus indica*
Trifolium amplectens
Trifolium tridentatum
Trifolium ciliolatum
Trifolium gracilentum
Trifolium albopurpureum
Trifolium microcephalum
****Erodium sp.*
Lotus subpinnatus
***Eremocarpus setigerus*
****Torilis nodosa*
***Anagallis arvensis*
Dodecatheon hendersonii
***Amsinckia douglasiana*
Gilia peduncularis
****Plagiobothrys canescens*
Plagiobothrys nothofulvus
Trichostema lanceolatum
Orthocarpus pusillus
Orthocarpus erianthus
Plantago erecta
Plectritis macrocerca
Plectritis ciliosa
***Hemizonia virgata*
Lessingia hololeuca
Baeria chrysostema
****Silybum marianum*
Achillea millefolium
****Centaurea melitensis*
****Centaurea solstitialis*

Other items of squirrel food included the fruits of live oak, buckeye, coffee berry and elder, obtained principally from the margins of the grazed areas, as well as grasshoppers (*Melanoplus devastator*), which abounded in the open throughout the summer and fall. During this study, food was always available in abundance for the squirrels.

The scattered occurrence of squirrel habitat and our limited personnel made it necessary to restrict trapping operations to four small areas totalling 77.6 acres in extent, all at the northern end of the reservoir (Plate 2):

Area A (observation area). On the steep hills just east of the dam; about 8.2 acres; bounded by trees and brush on the north, west and south, open grassland on the east; most thoroughly studied of all areas; excellent for close observation of squirrels; no squirrels removed at any time during the study.

Area B. Dam and immediate environs; about 19.8 acres; bounded by trees and brush on north and east, by reservoir on south, and by open grassland on west; more squirrels trapped here than in any other area; supplied most of those used for laboratory experiments.

Area C. Along upper levels of hills east of the dam, approximately 1500 feet above sea-level; about 32.7 acres; trees and brush scattered on east and west, open grassland on north and south; least well-defined of all areas; trapping discontinued after 1940.

Area D. A large horse pasture along the reservoir shore one-half mile south

of the dam; about 16.9 acres; trees and brush on north-east, open grassland on south, reservoir on west; of all areas the least densely populated by squirrels and the least thoroughly trapped; provided several records of unusual movement; a few squirrels removed in 1940 and 1941; trapping discontinued after 1941.

METHODS

Traps.—Live traps manufactured by Young's Animal Trap Company of Sunnyvale, California, were used throughout the study. These were of two sizes, 4 x 4 x 16 inches and 5 x 5 x 20 inches, made of heavy wire screen of $\frac{1}{3}$ inch mesh. A central treadle stands just above the floor, and there are two end gates that are raised when the trap is set. An entering animal depresses the treadle, thereby releasing the gates, to close both ends of the trap. Whole oat groats proved to be one of the best baits, although sunflower seeds were quite attractive in winter and early spring.

Traps were generally placed where likely to catch squirrels. In some cases they were scattered irregularly and in others were placed on a definite line but at varying intervals. The grid system of trapping was not employed, as it did not seem to lend itself readily to either the type of habitat or the activities of the squirrels. During hot weather shelters were constructed over the traps to protect the animals from direct sunlight; on several occasions exposure of less than two hours proved fatal. Trapping was carried on in Area A for about one week each month in which the field station was operated, in other areas less regularly but at least once in every six weeks; operations occasionally extended over an entire month. Trapping was usually continued in an area until all captures in one day were those of individuals taken at least once previously in that trapping period.

The 433 squirrels marked in 1940 were captured a total of 2,612 times in that year, an average of 6 captures per squirrel. The 461 squirrels studied in 1941 were taken 2,016 times, an average of 4.4 captures per squirrel. One female was taken 144 times over a 24 month period.

Handling.—A small bag, about 8 x 14 inches, of heavy fish netting (1-inch mesh measured at stretch) proved satisfactory for holding squirrels when they were being weighed or otherwise handled, although they would gnaw their way out if left for a short time.

To obtain a count of the ectoparasite fauna, a squirrel was placed in a large-mouthed, two-quart glass "Mason" jar. This was quickly capped and chloroform was introduced by an atomiser through a small hole in the cap to anesthetize both host and parasites; the latter then were readily combed from the squirrel into a large pan. Care in administering the proper dose was necessary, but some squirrels were anesthetized many times at weekly intervals without apparent adverse effects.

Weight records were taken for all squirrels caught, by use of a small spring scale, graduated in 25-gram intervals. Each animal was weighed at least once in every trapping period it was taken.

Marking.—Toe-clipping was the most reliable method used and gave permanent results in all cases. The distal joint was cut off with sharp surgical scissors, not more than one toe on each foot being removed. Infection incurred in a few

cases, but these recovered and no deaths were known from the operation. This familiar system is widely used and has already been described elsewhere (Ashbrook, 1936; Holdenried, 1940).

To test the efficiency of ear tagging, 95 "Salasco" aluminum fingerling fish tags were clipped into the right ear on male squirrels and the left ear on females, with results as follows:

Total tagged		95
Not caught again		18
Records inadequate		32
Tags definitely lost		26
Tags retained at last capture		19
90 days	6	
180 days	7	
270 days	1	
360 days	4	
450 days	1	

Within a week of tagging, scabs began to form around the places of insertion. That part of the pinna holding the tag frequently became infected and gradually sloughed away until the tag was lost. The average life of fingerling tags when rebent and used on fox squirrels (*Sciurus niger rufiventer*) was between one and two years (Baumgartner, 1940), but our experience does not recommend them for the permanent marking of ground squirrels.

Marks left by clipping the hair of restricted parts of the tail were visible at several hundred feet, as the squirrels usually held their tails off the ground and frequently raised them more or less perpendicularly. Such marks lasted until the hair was shed, which occurred once a year in the adults but several times in the first summer of life of the young. The method was quite helpful for temporary observation.

Other attempts at marking involved the use of dyes, supplied by the Nyanza Color and Chemical Company, including an aniline red and four fur dyes: black (Nyanzol D), brown (Nyanzol P), yellow brown (Nyanzol 2G) and reddish brown (Nyanzol 4R). The dyes were dissolved in boiling distilled water, cooled, and carried afield in half-pint jars; they were applied cold, and the fur dyes were fixed with hydrogen peroxide. Only restricted parts of a squirrel's body were dyed, such as the head, rump or tip of the tail. This method did not seem to have any adverse effect on the animals, and the individuals so marked did not appear to draw the attention of other squirrels. Results varied considerably as follows:

Brown: Of 5 squirrels dyed, 3 were recaptured; the dye was lost within 30 days.

Yellow brown: Of 7 squirrels dyed, 6 were recaptured; the dye was lost within 30 days.

Aniline red: Of 13 squirrels dyed, 10 were recaptured; in 7 cases the dye was lost within 30 days; 3 retained the dye for 30 days but lost it within 60 days.

Reddish brown: Of 17 squirrels dyed, 15 were recaptured; in 11 cases the dye was lost within 30 days; 2 retained the dye for 240 days, and 2 others for 330 days.

Black: Of 65 squirrels dyed, 50 were recaptured; in 15 cases the dye was lost within 30 days; 20 retained the dye for 60 days, 6 for 240 days, and 1 for 330 days.

Brown and yellow brown often failed to dye properly and also did not produce sufficient contrast with the natural color of the squirrels for them to be recognized at any distance. Aniline red was the most brilliant and could be seen from greater distances than any of the others, but faded quickly and usually was not visible after a few days of exposure to the sun. Reddish brown was a more durable color once the hair was actually dyed, but it proved difficult to fix. The most consistent and durable of all was black. The use of dyes to mark squirrels is apparently of limited value, but helpful when a few individuals are to be watched intensively.

SEASONAL CYCLE

The Beechey ground squirrel is primarily terrestrial, diurnal, and frequently gregarious in habit. It digs extensive burrow systems that serve for shelter in various ways, and for places in which to rear young. It has a regular seasonal cycle of activity, as outlined below.

Breeding season.—This is generally short and fairly well-defined; in the San Francisco Bay region it begins in February and is practically concluded by the middle of April (Grinnell and Dixon, 1918). At Calaveras Reservoir it was about ended when field work began (April 11, 1940; April 14, 1941). In the week of April 16 to 23, 1941, 29 females were taken, 6 pregnant (as judged by palpation) and 23 lactating. The last pregnant female was captured on April 23. Two late litters in 1941 suggested that some breeding occurred in May of that year. In southern California pregnant females have been taken in every month of the year (Storer, 1930).

In adult males at Calaveras Reservoir, reduction in size of testes was first noted in May, and by June the gonads had receded into the abdomen. In mid-October some adult males again showed testicular enlargement, and by the end of November the testes had descended in almost every male, adult or young. The testes remained large throughout the winter and spring.

With testicular recrudescence in the fall, the squirrels began to show more interest in each other and chases were more numerous. About this time a particular type of behavior was first seen (earliest observation—December 11, 1940). Squirrel A would chase squirrel B and face it when close; A would then place its head beside that of B, striking the latter on the neck or shoulders with the outer fore foot. This was repeated several times with their heads shifted from side to side. On the few occasions when the sexes could be distinguished, A proved to be a male and B a female.

Gestation.—An adult female taken on March 31, 1942, gave birth to young in the laboratory on April 20. The duration of gestation is not definitely known, but it has been estimated as about 30 days (Grinnell and Dixon, 1918). An estimate of 25 to 30 days has been made for *Citellus beecheyi douglasii* (Edge, 1931). In *C. columbianus* it is 24 to 25 days (Shaw, 1925) and in *C. tridecemlineatus* 27 to 28 days (Wade, 1927).

Birth and emergence of young.—Evidence cited above indicates that at Calaveras Reservoir most of the young were born by the middle of April. The

first young left their burrows on May 20, 1940, and May 26, 1941; nearly all had emerged by the middle of June. Edge (1931) found that the young of *C. b. douglasii* did not open their eyes until the fifth week or leave the burrow until the eighth week.

Lactation.—Our notes indicate a lactation period of 6 to 8 weeks. One adult female caught on April 16, 1941, had at least 6 embryos; on April 19 she was no longer pregnant but lactating; she continued to lactate until early June, but by June 24 her mammary glands and teats were far decreased, indicating that lacta-

FIG. 2. Growth in weight of ground squirrels at Calaveras Reservoir. Numbers indicate the total number of individuals on which each monthly average is based.

tion had ceased. Most of the adult females seemed to continue lactation after the young were out of the burrows; one allowed two young that had been out for about a week to nuzzle her teats and apparently nurse for a few seconds before she pushed them away. The young sometimes remained with their mother for at least two months after they first appeared above ground and for some time after lactation had stopped.

Growth.—These squirrels grew rapidly and reached a mature size by November when they were 7 to 8 months old. The average weights of young and adults at monthly intervals are shown in Figure 2. The lightest weight recorded for young just out of the burrow was 75 grams; the average was 100 grams. Within

one month the average rose to 200 grams, at which time (June) a more rapid weight increase became evident in the males; the young were then about two months old. This weight difference increased with age, and adult males averaged about 100 grams more than adult females. Mature squirrels generally weighed from 500 to 800 grams each. Weight increase continued throughout the winter and even following breeding; maximum weight did not coincide with attainment of sexual maturity. Adult squirrels were readily distinguished by weight from young of the season until the end of August, but after that the weight ranges overlapped and made age determination by this criterion difficult.

Molting.—Molting in young squirrels began within two weeks of emergence from the burrows, at which time their pelage was light-colored and quite sparse. The first dark coat was usually completed by July, before they had attained a weight of 300 grams. They continued to acquire new hair during the summer. Adult squirrels shed some hair throughout the year, but a definite molt was generally evident in May. At this time hair came out abundantly when the squirrels were handled, and bare patches of skin appeared through the pelage, particularly of females. The males seemed to have a rougher and more ragged coat and began to molt earlier. By the end of June almost every adult male had acquired new pelage. Females did not grow new hair until lactation had stopped, and their molting seemed to be more protracted; a few did not complete their new coat until August.

A general pattern was observed in the sequence of hair growth. New hair was usually first noticed on the crown, and then progressively along the back to the rump and tail; the shoulders and sides were next to acquire fresh hair, and the thighs were last. Ventral development was similar to dorsal; new hair on the tail grew in rapidly, to full length in four or five days.

Estivation-hibernation.—There were indications that at the Calaveras Reservoir some of the squirrels passed through a period of inactivity. A number of individuals marked and released in 1940 apparently disappeared in that season but were recovered in the same locality after trapping had been resumed in April 1941, as indicated below:

MONTH OF LAST CAPTURE IN 1940	ADULT ♂	ADULT ♀	YOUNG ♂	YOUNG ♀
May	0	1	—	—
June	0	2	—	—
July	1	3	—	—
August	1	3	2	1
September	3	4	0	2
October	0	1	0	8
November	1	1	4	2
December	4	1	10	12
Retaken in April 1941 or later	10	16	16	25

Trapping operations indicated that adult females showed the greatest tendency to disappear and were the first to do so; of the 16 adult females for which there are records, 6 had disappeared before August and 13 had apparently become inactive by the end of September. Adult males displayed a similar inclination,

though less markedly; 5 of 10 adult males with adequate records were not seen after September until their subsequent recapture in the spring. The activity of young squirrels was in sharp contrast to that of adults; of 41 young, only 5 were not caught after September and at least 22 were still active in December. These observations appear to substantiate the statement of Grinnell and Dixon (1918) that there is a period of hibernation or estivation, or the two combined, among some, at least, of the adult ground squirrels of this species.

REGULATION OF NUMBERS

The seasonal cycle with a short breeding season may be advantageous by limiting the period of greatest vulnerability, *i.e.* when the young are being reared, to a time of year otherwise favorable for growth, thereby tending to minimize the effects of disease and predation. In addition to the seasonal cycle, many other factors help to regulate the increase or decrease of population numbers. A few of these are discussed in this section.

Breeding population.—There was no evidence of females giving birth in the same season in which they were born, but almost every female had young the next season. Adults that survived into a second breeding season also gave birth. In any single breeding season there was no clearly defined non-breeding element, such as obtains in species that do not mature in one year. However, several adult females were observed that showed no evidence of pregnancy or lactation at any time during the season.

Number of litters per female per season.—It was evident at the Calaveras Reservoir that the majority, if not all, of the adult females had but one litter a year. Two late groups of young in 1941, which were not observed until July, possibly represented second litters, but in these cases the first litters were probably not raised. Grinnell and Dixon (1918) suggested that if two litters are born to a female in one season the second litter probably replaces loss of the first.

Number of embryos per female.—No data on this point were available from our study. An average of 7.2 embryos per female was reported from collections of more than 1000 squirrels examined each week from January 1 to June 4, 1910 (McCoy, 1912). An average of 8.2 embryos per female was obtained from 4,233 pregnant females taken in the vicinity of Los Angeles in 1925–26 (U. S. Publ. Health Serv., 1926). In the spring of 1923, 86 pregnant females from Tulare County averaged 9.9 embryos per individual (Jacobsen, 1923). All of these reports indicated wide ranges in the number of embryos per female (4 to 15) and considerable variation from month to month.

Prenatal mortality and number of young born.—Cases of probable fetal atrophy have been reported by Edge (1931) in *C. b. douglasii*. Little is known of prenatal mortality in wild animals, but it is probably a factor of considerable importance. In a study of wild rabbits, Brambell (1942) found that from 45 to 58 percent of all fertilized ova were lost before birth of the litter occurred.

Instances of 5 young born have been cited by Edge (1931) for *C. b. douglasii* and by Gander (1930) for *C. b. beecheyi*. It is likely that the number of young born is distinctly less than the number of implanted ova.

Mortality in burrows and number of young at emergence.—While still in the nest,

TABLE 1.—*Trapping statistics of ground squirrels studied at Calaveras Reservoir, 1940–1942*

	AGE AT FIRST CAPTURE				TOTAL
	Adults		Young		
	♂♂	♀♀	♂♂	♀♀	
1940: 542					
Marked:					
Area A	11	25	46	56	138
Area B	17	25	68	44	154
Area C	20	21	42	22	105
Area D	5	2	15	14	36
Total	53	73	171	136	433
Removed:					
Area B	0	0	43[1]	53[1]	96
Area D	1	8	0	4	13
Total	1	8	43	57	109
1941: 545					
Marked:					
Area A	0	1	69	66	136
Area B	5	26	76	81	188
Area D	0	0	0	5	5
Total	5	27	145	152	329[2]
Recovered from 1940:					
Area A	5	8	13	28	54
Area B	10	13	23	23	69
Area D	2	0	6	1	9
Total	17	21	42	52	132
Removed:					
Area B	3	19	30	14	66
Area D	1	6	9	2	18
Total	4	25	39	16	84
1942: 286					
Marked:					
Area A	0	2	47	32	81
Area B	6	10	42	48	106
Total	6	12	89	80	187
1942: 286					
Recovered from 1940:					
Area A	0	0	4	12	16
Area B	2	0	2	9	13
Recovered from 1941:					
Area A	0	0	12	16	28
Area B	1	7	4	18	30
Total	3	7	22	55	87[3]
Removed:					
Area B	4	8	0	0	12

[1] Age or sex doubtful in a few cases.

[2] 8 yg. ♂♂ and 12 yg. ♀♀ were removed late in 1941.

[3] 2 yg. ♂♂ and 6 yg. ♀♀ were removed early in 1942.

the young are especially subject to predation by snakes and other fossorial or digging animals. At the Calaveras Reservoir adult females were twice seen transferring their young to a fresh burrow; in one instance a rattlesnake that proved upon dissection to have fed on a young squirrel was found at the entrance of the old burrow.

Eight litter counts were made within a day or two of first emergence. One contained 9 young, 3 had 7, 3 had 6, and 1 had 2; the average was 6.25. The total numbers of marked squirrels (Table 1) indicated lower averages for the population as a whole (4.21 young per litter in 1940 and 3.00 in 1941) but mortality *after* emergence was probably responsible in part for the lower figures.

Disease.—No evidence of disease was observed in 1940 and 1941, but on eight occasions between June 11 and 26, 1942, fleas collected from ground squirrels proved to be infected with plague (*Pasteurella pestis*), and organs from several others were likewise positive. The presence of this disease in the Calaveras Reservoir area had been demonstrated in November 1933, when a rodent survey by the California Department of Public Health yielded a plague-infected squirrel. Epizootics of plague among ground squirrels of this species are well-known and evidently recur in the same areas after intervals of several years (Evans, Wheeler and Douglas, 1943). Although plague apparently did not occur in epizootic proportions at the Calaveras Reservoir in the period of this study, it is evidently established there in the ground squirrel population.

Predation.—Squirrel predators were abundant in the Calaveras Reservoir area. Of 14 Pacific rattlesnakes (*Crotalus viridis*) whose stomach contents were examined, 4 had eaten young ground squirrels. Red-tailed hawks (*Buteo jamaicensis*) were frequently seen diving at squirrels and there were two records of actual catch. Gray foxes (*Urocyon cinereoargenteus*) and bobcats (*Lynx rufus*) were both observed stalking squirrels, and several burrows were noticed that bore signs of excavation by badgers (*Taxidea taxus*). Other species that are known to prey on ground squirrels and that were seen in the area include the gopher snake (*Pituophis catanifer*), golden eagle (*Aquila chrysaetos*) marsh hawk (*Circus hudsonicus*), Cooper hawk (*Accipiter cooperi*), prairie falcon (*Falco mexicanus*), horned owl (*Bubo virginianus*), raccoon (*Procyon lotor*), weasel (*Mustela frenata*), and coyote (*Canis latrans*).

Poisoning.—The scattering of poisoned grain should also be mentioned as an important cause of ground squirrel destruction. Poisoning operations had been carried out annually in the Calaveras Reservoir area since the 1933 plague survey but were discontinued for the duration of the present study.

POPULATION STATISTICS

Trapping operations were sufficiently frequent and on a scale large enough to provide a rough census of the squirrel population. As a census technique, however, trapping is subject to many errors. The presence of baited traps in an area may produce unusual movements or local disturbances; one sex or age group may be more easily trapped than another. In the present study, the amount of trapping varied from year to year and in the different Areas was

correlated neither with the size of the area nor with the density of squirrels. The following figures based on trapping do not claim to represent the precise state of the squirrel population, but they can be accepted as satisfactory indications of trends.

Density.—The total area trapped in 1940 was estimated at 77.6 acres and the total number of squirrels taken was 542. This indicates an average density of 7 squirrels per acre. However, the different trapping areas showed great variation in density (squirrels per acre), as indicated in Table 2. Comparable data for 1941 and 1942 are not available for all areas, but Areas A and B were trapped to approximately the same extent for the three successive years, with density figures as in Table 3. Despite removals of squirrels from Area B in 1940 and 1941, both Areas showed a marked increase in density in 1941 and a definite

TABLE 2.—*Density of ground squirrel population in trapping areas in 1940*

	ESTIMATED ACREAGE	NO. CAUGHT	DENSITY
Area A	8.2	138	16.8
Area B	19.8	250	12.6
Area C	32.7	105	3.2
Area D	16.9	49	2.9
Total	77.6	542	7.0

TABLE 3.—*Density of ground squirrel population in Areas A and B, 1940–1942*

	1940		1941		1942	
	Number	Density	Number	Density	Number	Density
Area A	138	16.8	190	23.1	125	15.2
Area B	250	12.6	323	16.3	161	8.1
Total	388	13.9	513	18.3	286	10.1

decrease in 1942. These changes appeared to be representative of the Calaveras Reservoir area as a whole. A real decline in numbers was largely responsible for the decrease in 1942, but a short trapping season in that year may also have had some effect on the figures.

Sex Ratios.—The 762 squirrels marked in 1940 and 1941 included 374 males and 388 females, a sex ratio of 96.4 males per 100 females. Analysis by age groups indicated a decided difference in the sex ratios of marked young and adult squirrels, as shown in Table 4.

Combined figures for 1940 and 1941 gave a ratio of 109.7 males per 100 females among the young, and only 67.6 males per 100 females among the adults. The relatively fewer number of males in the adult population suggests a greater survival of females. The development of this trend is shown in more detail in the analysis of young squirrels marked in Areas A and B, presented in Table 5.

The decrease of males is quite evident in the figures for 1941. In June, when the young squirrels were first caught, there were nearly as many males as females, but the ratio had fallen considerably by September, and in the following April, when they were adults, there were only half as many males as females. In April 1940, the adult population of Area A consisted of 11 males and 25 females; in April 1941, of 18 males and 36 females; in April 1942, of 16 males and 28 females. Differences in behavior, as discussed in a later section, may help to explain this apparent difference in sex survival.

Age Ratios.—Adult squirrels were distinguished with considerable success from young of the year, but more precise determination of age was possible only

TABLE 4.—*Sex ratios of marked young and adult squirrels, 1940–1941*

	YOUNG			ADULT		
	1940	1941	Total	1940	1941	Total
Number	307	297	604	126	164	290
Males per 100 females	125.7	95.4	109.7	72.6	64.0	67.6

TABLE 5.—*Changes in sex ratios of young squirrels marked in Areas A and B*

	JUNE	SEPTEMBER	DECEMBER	APRIL (OF NEXT YEAR)
Young Marked in 1940				
Males	114	70	54	36
Females	100	75	59	51
Males per 100 females	114	93.3	91.5	70.6
Young Marked in 1941				
Males	145	50	29	16
Females	147	85	52	34
Males per 100 females	98.6	58.8	55.8	47.1

in the case of marked individuals. The 1940 population of 433 squirrels marked on all Areas was composed of 307 young and 126 adults, an age ratio of 244 young per 100 adults. The 1941 population, including recoveries from 1940 as well as those marked in 1941, comprised 297 young and 164 adults, an age ratio of 181 young per 100 adults. The age ratio at different seasons of the year was examined to determine the relative survival of the two age groups. Seasonal changes in age ratio (young per 100 adults) are shown in the data of squirrels marked in Areas A and B, presented in Table 6. There was apparently some change of age ratio in the period from June 1940 to April 1941, and from June 1941 to April 1942 the number of young per 100 adults dropped from 254 to 143. This decrease of young squirrels suggests the operation of a selective mortality factor in 1941 or early 1942. Among several possible causes, plague

may have contributed to this decimation, since it was demonstrated in the area in 1942 and since young squirrels are known to be more susceptible to this disease than are adults.

Longevity.—The life-time of a squirrel, if it dies of old age, has been estimated as five years (Grinnell and Dixon, 1918). At the Calaveras Reservoir two males born in 1939 (or earlier) were marked in 1940 and last recaptured in the summer of 1942; their age at last capture was, therefore, three years or more. There were also 36 squirrels born in 1940 that were recovered in 1942, at an age of two years.

Of the 292 squirrels marked in Areas A and B in 1940, 123 were recaptured in 1941 and 29 in 1942, a survival of 42 and 10 percent respectively. Of the 324 marked in 1941, 58 (18 percent) were recovered in 1942. These figures are too incomplete for statistical treatment, but it seems improbable that the life expectancy of these squirrels was more than two years.

TABLE 6.—*Changes in age ratios of squirrels marked in Areas A and B*

	JUNE	SEPTEMBER	DECEMBER	APRIL (OF NEXT YEAR)
Marked in 1940				
Young	214	145	113	87
Adults	72	47	43	36
Young per 100 adults	297	309	263	242
Marked in 1941				
Young	292	135	81	50
Adults	115	50	41	35
Young per 100 adults	254	270	198	143

Population fluctuation.—Area A was sufficiently well trapped to indicate progressive changes in the numbers of squirrels and the main characteristics of the population curve; the data are presented in Table 7 and graphically in Figure 3. The young squirrels are represented as appearing in the population in June, the month in which the majority of them came to the surface and were first caught.

Eleven adult males and 25 adult females were known to be alive in the Area in April 1940; this group of 36 was the remnant population from the previous year. They gradually disappeared or died, so that by the following April there were only 5 males and 8 females of this group; none was known to survive after November 1941. In June 1940, 46 young males and 56 young females were added to the marked population. These likewise declined in numbers; 13 males and 28 females survived until the following April, and 4 males and 12 females were still alive in April 1942. The 1941 season produced 69 males and 66 females; this group apparently suffered heavy losses, for only 12 males and 16 females were known to be alive in April 1942.

It is clear that there was a sharp upswing in the ground squirrel population curve every spring, due to the birth of the young within a short season; this was followed by a compensatory annual decline. This type of population curve differs markedly from that of a species such as *Peromyscus maniculatus*, with a

TABLE 7.—*Survival of ground squirrels marked on Area A from April 1940 to July 1942*

	ADULTS OF 1940		YOUNG OF 1940		YOUNG OF 1941		TOTALS
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	
1940							
April	11	25					36
May	11	24					35
June	11	21	46	56			134
July	10	17	36	52			115
August	9	15	25	48			97
September	8	11	21	45			85
October	8	9	21	40			78
November*							
December	8	9	20	33			70
1941							
January*							
February*							
March*							
April	5	8	13	28			54
May	5	8	13	27			53
June	4	8	9	25	69	66	181
July*							
August	2	4	7	17	59	63	152
September	2	1	6	15	37	52	113
October*							
November	2	0	6	14	25	32	79
December*							
1942							
January*							
February*							
March*							
April			4	12	12	16	44
May			3	11	12	16	42
June			2	9	12	13	36
July			1	7	11	7	26

* Indicates no trapping done.

protracted breeding season and several litters per year, where births throughout the season tend to offset the effects of mortality and thus help to stabilize seasonal fluctuations.

The number of adult individuals alive in the breeding season can be used as an index of annual increase or decrease of the squirrel population. In Area A,

the adult population in April 1940 consisted of 36 individuals (11 males, 25 females); in April 1941 of 54 (18 males, 36 females); and in April 1942 of 44 (16 males, 28 females). In 1941 this group evidently increased 50 percent over that of the previous year, but in 1942 suffered an 18 percent decrease; this decline was apparently due to the heavy losses among the young of 1941. The net result in the two years 1940–1 and 1941–2 was an increase of 22 percent in the adult population. A greater increase might well have been expected, in view of the cessation of human control measures during the study and the high breeding

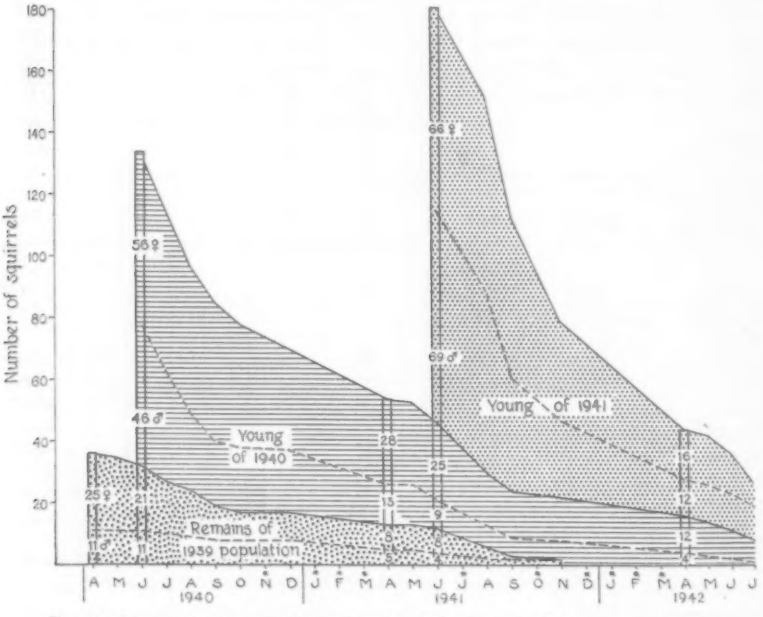

FIG. 3. Changes in the numbers of squirrels in Area A, Calaveras Reservoir.

potential which this species is generally considered to possess. The influence of emigration and immigration will be considered below.

HOME RANGE AND MOVEMENTS

One of the chief objects of the study was to determine the extent to which ground squirrels move about and the size of individual ranges. For this we had to rely largely upon the information provided by trapping, which at its best is incomplete and needs to be interpreted with care. Of the 762 squirrels marked in 1940 and 1941, 221 were not recaptured after marking, and 114 others proved unsatisfactory for recording either range or movement because of insufficient

data. The remaining 427 squirrels furnished the following information, based on the greatest distance between points of capture:

MAXIMUM MOVEMENT IN YARDS	NUMBER OF SQUIRRELS
0–150	293
150–300	53
300–600	54
600–1200	21
1200 or more	6

Nearly 70 percent of this group were never trapped outside areas of 150 yards in greatest length. A small range was further suggested by the local distribution of burrows; many apparently suitable localities within the grassland habitat were unoccupied although adjacent to inhabited areas. Grinnell and Dixon (1918) wrote that as a result of this "tendency to occupy certain definite tracts within a general territory to the exclusion of intervening places, and this without obvious reason as regards food supply and kind of soil . . . centers of population may arise through the historical circumstance of original settlement by first-comers." At the Calaveras Reservoir, previously existing burrow systems seemed to play a part in the current distribution of squirrels; old, discarded burrows were frequently dug out again and occupied, but no completely new burrows were observed. The squirrels tended to group in "colonies" where burrow systems were available. These comprised from 5 or 6 to as many as 45 or 50 adult squirrels.

Home range.—Some species of animals lead a nomadic existence; others confine their activities to a relatively small area, frequently referred to as the home range. In some instances this home range is maintained permanently in one locality; however, in many cases it is transferred to new areas, sometimes with considerable regularity, as in migration. These changes render the measurement of home ranges difficult. In the case of the ground squirrels studied at the Calaveras Reservoir, occupation of an area for a period of at least one month was considered necessary to fulfill the requirements of a definition of home range. The term as it is applied here refers to the territory covered above ground and does not include the underground burrow systems, sometimes 50 feet and more in extent, which were inaccessible for study.

Our observations indicated that there were usually several burrow entrances within the range of a single squirrel; some of these led to the same burrow system. As far as could be determined, individuals normally inhabited but one system at a time, frequently using one particular entrance; some systems evidently housed several squirrels.

The most satisfactory estimates of home range were obtained in Area A, for no squirrels were removed from it at any time; trapping operations were more thorough and complete than in any other Area, and in 1940 one day per week was devoted to observation from a blind. The trap sites in Area A are indicated in Figure 4. In 1940 this Area (8.2 acres) was covered by 46 traps (Nos. 1–46);

the majority of these were retained at the same sites in 1941 and a few more (Nos. 201–208) added. The greatest distance between traps was less than 50 yards and most of them were much closer together. All traps were in use on each trapping day and were inspected at least twice daily.

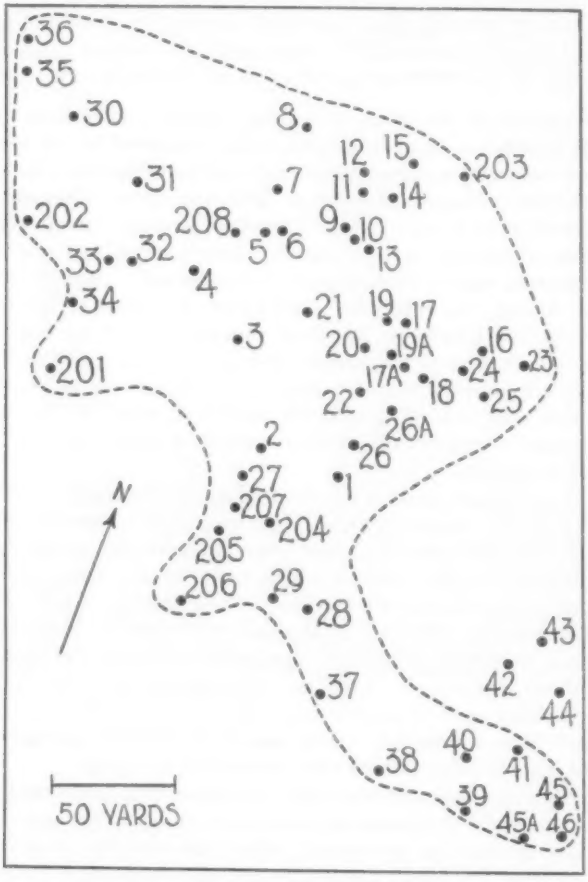

FIG. 4. Locations of trap sites in Area A, Calaveras Reservoir.

Table 1 shows that in 1940 a total of 138 squirrels was marked in Area A. The records of 32 of these are too short to be analyzed for range or movement, but the remaining 106 were classified into five groups according to the behavior displayed in the maintenance of individual ranges, as indicated here with illustrative case histories.

(1) *Restricted to a small range.*—(Adults—9 males, 14 females. Young—10 males, 22 females.) This was the largest group and included 52 percent of the records which were analyzed; they occupied ranges of 150 yards or less in greatest length, and were never taken outside their ranges. In some cases records extended up to 27 months.

Ad. Male No. 7. Range—0.63 acre; 125 yds. in greatest length. 1940: April 29–Dec. 11 (caught 38 times, at traps 36, 31, 30, 33, 32, 5, 35). 1941: April 17–Nov. 19 (22 times—traps 36, 201, 35, 30, 202, 33).
Ad. Female No. 24. Range—0.30 acre; 85 yds. in greatest length. 1940: June 10–Sept. 27 (7 times—traps 28, 29, 37). 1941: Apr. 17–Aug. 21 (15 times—traps 28, 29, 37, 204).
Yg. Male No. 40. Range—0.66 acre; 85 yds. in greatest length. 1940: Aug. 20–Dec. 10 (10 times—traps 27, 28, 1, 2, 29). 1941: Apr. 17–June 24 (14 times—traps 204, 206, 205, 207, 27).
Yg. Female No. 42. Range—0.30 acre; 50 yds. in greatest length. 1940: July 4–Oct. 31 (24 times—traps 8, 9, 11, 15, 12). 1941: Apr. 19–May 12 (5 times—traps 8, 12).

(2) *Shifted range slightly.*—(Adults—1 male, 3 females. Young—2 males' 4 females.) This group made a definite shift in range, moving as much as 150 yards from the previous territory but remaining within the same general locality.

Ad. Male No. 5. 1940: Apr. 23–Oct. 27 (10 times–traps 2, 29, 28, 27, 26, 37). Range—0.84 acre; 100 yds. in greatest length. Dec. 5–10 (3 times—trap 11); had moved 100 yds. 1941: Apr. 17–Nov. 18 (21 times—traps 8, 7, 12, 15, 14, 13, 9, 6). Range—0.54 acre; 65 yds. in greatest length.
Ad. Female No. 1. 1940: Apr. 17–May 1 (5 times—traps 16, 23). May 9–Aug. 20 (24 times—traps 28, 29, 37); had moved 135 yds. Aug. 21–Sept. 5 (14 times—traps 1, 26, 29, 28, 2, 27). Range—0.66 acre; 65 yds. in greatest length.
Yg. Female No. 43. 1940: July 4–Dec. 9 (22 times—traps 23, 15, 11, 16, 14, 18). Range—1.02 acres; 100 yds. in greatest length. 1941: Apr. 17–Aug. 10 (19 times—traps 15, 23, 204, 16, 17A, 13). Range—1.02 acres; 100 yds. in greatest length. Aug. 10–23 (6 times—traps 41, 45A); had moved 150 yds. 1942: June 4–24 (3 times—traps 46, 41).

(3) *Occasionally taken far from usual range.*—(Adults—3 females. Young—3 males, 9 females.) These squirrels normally occupied a small range but were occasionally caught 300 yards or more afield.

Ad. Female No. 4. Range—0.54 acre; 100 yds. in greatest length. 1940: Apr. 23 (trap 17); May 24 (trap 28); June 13 (Area B); June 13–17 (traps 1, 2); June 20 (Area B); June 21 (trap 37); Aug. 19–21 (traps 27, 28, 1). Taken 330 yds. from normal range.
Yg. Male No. 33. Range—1.80 acres; 175 yds. in greatest length. 1940: July 1–Dec. 12 (44 times—traps 20, 14, 9, 25, 26, 29, 17, 13, 1, 28, 2, 27, 23, 22, 18). Taken Sept. 14 in Area B, 300 yds. from normal range.
Yg. Female No. 40. Range—0.30 acre; 50 yds. in greatest length. 1940: July 3–Dec. 9 (16 times—traps 4, 5, 21, 6). Taken Sept. 10 and 15 in Area B, 330 yds. from normal range.

(4) *Permanent transfer of range.*—(Adults—1 male. Young—6 males, 6 females.) These moved from 300 to 1200 yards to Areas B, C, or D and established themselves there. To this group doubtless belong some squirrels not recaptured after marking.

Yg. Male No. 22. 1940: June 11–Sept. 4 (12 times—traps 5, 3, 2, 4, 21, 6). Range—0.66 acre; 100 yds. in greatest length. Taken July 29 at trap 41 and Aug. 13 in Area B. Sept. 7–Nov. 13 (22 times—Area B); distance moved—700 yds. 1941: Apr. 17–Oct. 29 (27 times—Area B). 1942: Apr. 2 (Area B).
Yg. Female No. 32. 1940: June 29–Aug. 5 (8 times—traps 29, 18). Aug. 12–Oct. 25 (10 times—Area B), distance moved—300 yds. 1941: Apr. 18–June 21 (8 times—Area B). 1942: June 17 (Area B).

(5) *Larger immature ranges followed by smaller adult ones.*—(Young—5 males, 3 females). This group consisted of individuals that maintained ranges up to 300 yards as young squirrels, but which eventually settled down to smaller ranges that they occupied as adults. Five other young (4 males, 1 female) with similar large ranges but no adult records are presumably referable to this category.

Yg. Male No. 5. Immature range—3.24 acres; 360 yds. in greatest length. Adult range—0.24 acre; 40 yds. in greatest length. 1940: June 2–Sept. 5 (19 times—traps 12, 30, 38, 39, 46, 41, 37, 45A, 45, 28, 2). Sept. 20–Nov. 16 (12 times—traps 45A, 46, 45). 1941: Apr. 18–Sept. 27 (13 times—traps 46, 45A, 45). 1942: June 4–July 18 (4 times—traps 46, 39, 45).
Yg. Male No. 23. Immature range—1.32 acres; 225 yds. in greatest length. Adult range—0.54 acre; 75 yds. in greatest length. 1940: June 11–Dec. 11 (21 times—traps 23, 14, 15, 37, 25, 16). 1941: Apr. 16–Sept. 28 (11 times—traps 23, 22, 25, 16, 26A, 18). 1942: May 24–Aug. 27 (5 times—traps 25, 26A, 1).

The most striking examples of limited range were observed among the adult males, of which 21 (including some young with subsequent adult records) were caught in Area A from April 17, 1940 to June 29, 1941. None was taken or observed more than 150 yards from the point at which it was marked, excepting No. 5, which shifted its range, and No. 9, which moved to Area B and established itself there. The ranges of these squirrels are indicated in Figure 5, grouped in periods of approximately three months each and based on the trap positions at which animals were taken; outlines of range are given only for individuals caught five or more times in any period. The average range was 0.36 (0.06–0.74) acre in extent and 75 (15–135) yards in greatest length. Adult males evidently were restricted closely to small ranges, which seldom overlapped; in the few cases where there was partial coincidence of range, the invading squirrel was generally taken only once or twice within the range of the established individual.

The ranges of 51 adult females caught in Area A are similarly shown in Figure 6. These appeared to be somewhat larger than those of adult males, averaging 0.59 (0.12–1.62) acre in extent and 95 (25–225) yards in greatest length. Like the males, most of the adult females apparently remained within their normal ranges, although there were several (such as Nos. 4 and 21) that visited Area B and others (such as Nos. 1 and 16) that shifted their range from time to time. In contrast to the males, however, adult females frequently overlapped in their ranges, in some cases completely (Nos. 31 and 47, and Nos. 43 and 52).

The range of young squirrels centered at first around the burrow in which

they were weaned. For the first week or so after emergence they rarely strayed more than a few yards from the burrow entrance, but as they grew larger this range increased rapidly. Some moved to other Areas, but many remained in Area A and were never taken far from the locality at which they had been marked.

In summary, observations at the Calaveras Reservoir indicated that many ground squirrels remained within a small area throughout much of their lives. This sedentary behavior may help to explain the frequent occurrence of unoccupied territory apparently suitable for habitation.

Movements.—Records showing a total distance covered of more than 150 yards were analyzed for movements. The 134 squirrels in this category represented 17.6 percent of the marked population (762 individuals) and 31.4 percent of the group with adequate range or movement records (427 individuals). None of the movements observed was very extensive; only six individuals were known to have moved 1200 yards or more, and the maximum distance recorded was about 1300 yards. It is likely that some individuals moved out of range of the traps, but there was no indication of large-scale emigration over great distances. No reports of mass movements among ground squirrels of this species are known to us, such as have been observed in the eastern gray squirrel *Sciurus carolinensis* (Seton, 1929).

Movements were occasionally accomplished in a very short time, but sometimes lasted over several weeks or even months. This difference in activity is illustrated by the following examples:

Ad. Female No. 4. 1940: June 13 at 3:30 p.m. (Area B); at 6:15 p.m. (trap 1). Distance moved—330 yds.
Yg. Female No. 48. 1940: July 19 (trap 41); Aug. 26 (trap 45); Aug. 27 (trap 37); Sept. 28 (trap 29); Dec. 8 (trap 15). Distance moved—350 yds.

In 36 of 73 cases recorded in 1940, movement was followed by return to the original or marking locality, where permanent residence was resumed. The purpose of such movements is not clear, but they were apparently exploratory in nature. Permanent transfer of range was indicated for 15 adults and 29 young which remained in new localities for at least one month after movement away from their marking areas.

The month in which movement took place is known for 84 squirrels, as follows:

MONTH OF MOVEMENT	ADULT ♂	ADULT ♀	YOUNG ♂	YOUNG ♀
April	1	1	—	—
May	1	0	—	—
June	4	4	4	0
July	0	3	10	4
August	1	4	16	5
September	0	0	13	5
October	2	0	2	2
November	0	0	1	0
December	0	0	0	1

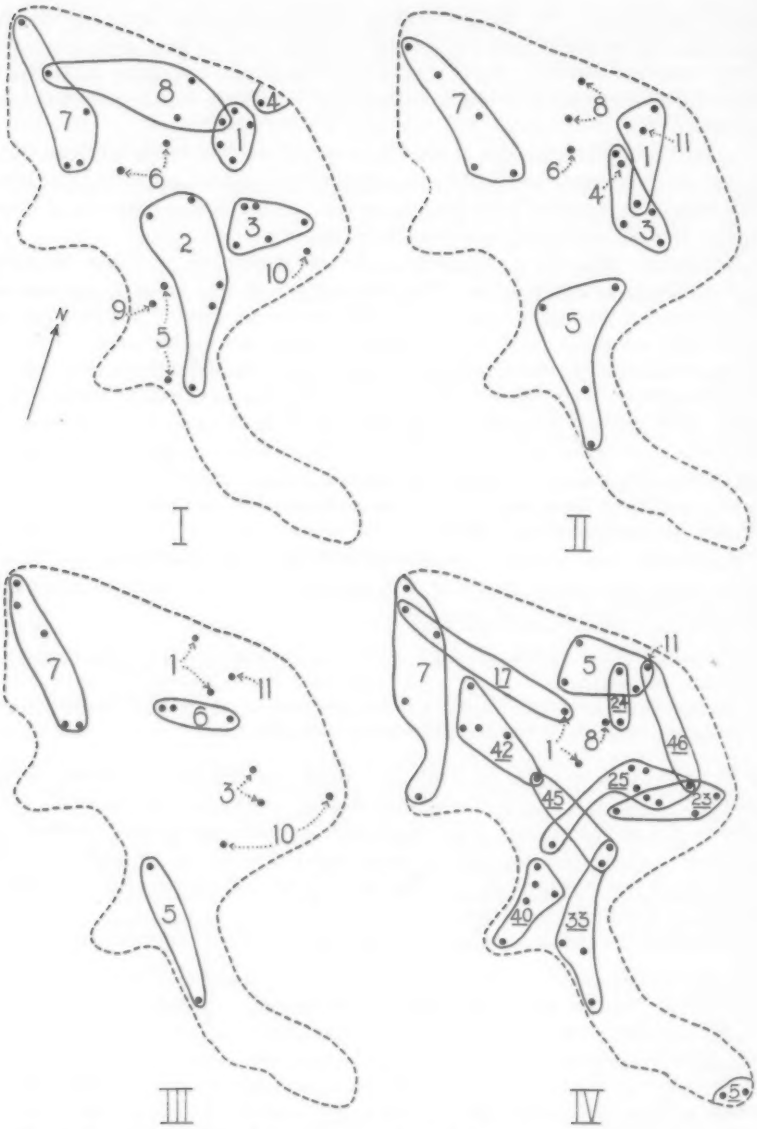

FIG. 5. Home ranges of adult male ground squirrels in Area A, Calaveras Reservoir, 1940–1941. I: April 17 to June 30, 1940—45 trapping days. II: July 1 to September 29, 1940—41 trapping days. III: October 1 to December 12, 1940—23 trapping days. IV: April 16 to June 29, 1941—30 trapping days. Numbers refer to serial number of squirrels; underscored numbers indicate squirrels marked as young in 1940.

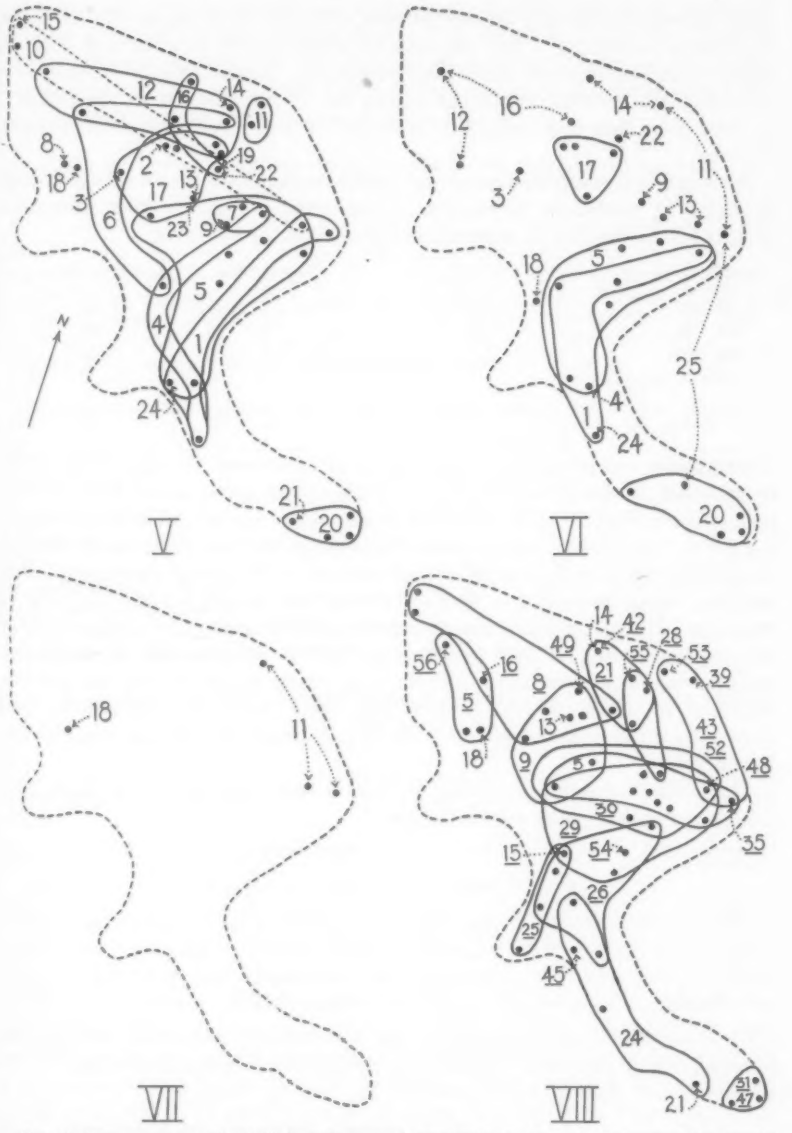

FIG. 6. Home ranges of adult female ground squirrels in Area A, Calaveras Reservoir, 1940–1941. V: April 17 to June 30, 1940—45 trapping days. VI: July 1 to September 29, 1940—41 trapping days. VII: October 1 to December 12, 1940—23 trapping days. VIII: April 16 to June 29, 1941—30 trapping days. Numbers refer to serial number of squirrels; underscored numbers indicate squirrels marked as young in 1940.

Some difference evidently existed between adult and young squirrels with regard to time of movement. The majority of adults moved in June and July, by which time breeding and lactation had ceased. August and September were the months of greatest movement among the young; this was in the period of activity after they had become independent of their mothers and the parental burrows.

A comparison of age and sex groups indicates that there was a relatively high incidence of movement among the young males. The age when movement occurred is known for 113 squirrels, as indicated in the following:

DISTANCE MOVED (YARDS)	ADULT ♂	ADULT ♀	YOUNG ♂	YOUNG ♀
150–300	8	10	16	9
300–600	2	10	24	11
600–1200	1	0	14	4
1200 or more	1	0	2	1
Totals	12	20	56	25

Young males comprised the largest group of movement records, which might be expected, because they also made up the largest group in the total marked population (Table 1). The incidence of movement can be obtained by comparing the *percentage* showing movement in each age and sex group as in Table 8. About 35 percent of the adults and 50 percent of the young disappeared after marking, either because they died or because they moved beyond the range of trapping. Hence it is likely that each group actually contained a higher percent showing movement. This is indicated in Table 9. Either basis of comparison leads to the same conclusion, namely that young males showed the greatest tendency to move. Similar observations were made by Kalabukhov and Raevskii (1935) in population studies of a Russian ground squirrel (*Citellus pygmaeus*).

The number of squirrels marked in 1940 in each Area that were taken later that year in other Areas was as follows:

AREA OF MARKING	AREA OF RECAPTURE A	B	C	D	TOTALS
A	—	20	15	1	36
B	11	—	5	1	17
C	2	5	—	3	10
D	0	0	1	—	1
Totals	13	25	21	5	64

From these figures a *movement index* was devised for each Area by dividing the emigration from the Area (totals at the right of the horizontal columns) by the migration into that Area (totals below the vertical columns):

$$\text{Movement index of Area A} = \frac{\text{No. of squirrels marked in Area A that were subsequently caught in other areas}}{\text{No. of squirrels marked in other areas that were subsequently caught in Area A}}$$

The movement indices and the corresponding population densities (squirrels per acre) of the different Areas are compared as shown in Table 10. Area A, with the greatest density, also had the highest movement index; Area D, the least density and the lowest index. Movements thus appeared to be *away* from areas of higher density *towards* those of lower density.

TABLE 8.—*Percent of total population, marked in 1940–1941, showing movement*

	ADULT		YOUNG	
	♂	♀	♂	♀
Total marked population (1940–1941)	117*	173*	316	288
Number showing movement	12	20	56	25
Percent showing movement	10.3	11.6	17.7	8.6

* Includes recoveries in 1941 of squirrels marked in 1940.

TABLE 9.—*Percent of population with adequate records, marked in 1940–1941, showing movement*

	ADULT		YOUNG	
	♂	♀	♂	♀
Total population with adequate records (1940–1941)	78*	110*	157	148
Number showing movement	12	20	56	25
Percent showing movement	15.4	18.2	35.7	16.9

* Includes recoveries in 1941 of squirrels marked in 1940.

TABLE 10.—*Comparison of the trapping areas in regard to movement indices and population density*

1940	A	B	C	D
Movement index	2.77	.68	.48	.20
Density	16.8	12.6	3.2	2.9

SOCIAL BEHAVIOR AND TERRITORIALISM

Some squirrels regularly inhabited a common burrow system without apparent conflict, but on several occasions when individuals were frightened into burrows evidently not their own, squeals and other signs of conflict were heard and the intruder was evicted. Every squirrel had three glandular folds just anterior to the anus, which apparently served as a means of identification; they were extruded when the animal was excited or frightened, and when two squirrels met, each smelled the anal region of the other. Young squirrels sometimes tolerated each other and sometimes gave chase, apparently in play; they were generally interested in the approach of any squirrel, young or adult. Adult females were seldom seen to chase young, and pursued other adults seemingly with little vigor or determination. The ranges of young squirrels and of adult

females frequently overlapped, but there was little evidence of fighting among them.

Adult males displayed a greater degree of aggressiveness. They generally tolerated the very young squirrels and allowed the latter to forage peacefully beside them, but by mid-summer adult males were frequently observed to chase all young that came near them. They chased other adults at all times, but especially in April and early May (no observations were made from January to April). Fighting that resulted in open wounds was never actually observed, but of 55 adult males captured between April and June 1941, 21 had visible scars on their heads or bodies, apparent marks of conflicts, which might have taken place below ground. Females were rarely found with such scars. The possibility that adult males maintained individual territories, which they defended against invasion by other males, is suggested by the following evidence: (1) They possessed comparatively small ranges to which they steadily adhered. (2) Their ranges, though adjacent, seldom overlapped; the occasional overlaps were slight. (3) They were much more aggressive than adult females or young, and vigorously chased other squirrels. (4) Many of them showed scars. (5) The relative scarcity of adult males as compared with adult females suggests that the former were excluded from established territories and forced to move to other areas; this would naturally lead to lower densities of adult males in colonized areas. Grinnell and Dixon (1918) believed that in the breeding season adult males occupied individual burrows at the outskirts of a colony. The majority of our observations were not made in the breeding season proper, but they indicate that territorialism, if it exists, may extend to other parts of the year.

SUMMARY

1. This paper presents a three-year population study of the Beechey ground squirrel at the Calaveras Reservoir in central California. A total of 1,154 squirrels was caught, of which 949 were marked and released for further observation.

2. The study area is in the Upper Sonoran life-zone and has a mild climate with a pronounced wet season. Ground squirrels were largely restricted to open grasslands, where abundant food was available at all seasons. Four areas (A, B, C, and D), from 8.2 to 32.7 acres in extent and with a total acreage of 77.6, were selected for trapping and marking squirrels.

3. Live traps of heavy wire screen were used, and generally placed where likely to catch squirrels instead of in a grid system. Squirrels were weighed and marked before being released. Toe clipping proved to be a thoroughly reliable marking method. Ear tags and dyes were also employed to mark squirrels, but were not very satisfactory.

4. The Beechey ground squirrel has a marked seasonal cycle of activity in this area, breeding probably from February to April. Young squirrels first left their burrows late in May, but grew rapidly and attained mature size by November, when 7 to 8 months old; mature squirrels generally weighed from

500 to 800 grams each. Young squirrels acquired new hair throughout the summer, and a definite molt in adults was generally evident in May. Trapping records indicated that some of the adults, particularly females, entered a period of estivation and/or hibernation, but that many of the young were active throughout the year.

5. In the breeding season almost every female apparently gave birth to a single little of young. Eight litter counts made within a day or two of first appearance above ground gave an average of 6.25 young per litter. Among mortality factors presumed to be acting on this population were disease, present in 1942 in the form of plague (*Pasteurella pestis*), and predation by many vertebrate species.

6. In 1940 there was an average density of seven squirrels per acre on the total area trapped; figures for Areas A and B indicated an increase in density in 1941 and a decrease in 1942. Analysis of sex and age ratios suggested a greater survival of female squirrels and pointed to the operation of a selective mortality factor in 1941 or early 1942, which reduced the population of young. Only two individuals were known to have attained an age of three years, and it is unlikely that the average life-time under natural conditions was more than two years. In Area A there was a net increase of 22 percent of squirrels from 1940 to 1942, as indicated by the number of adults alive in the breeding season.

7. Nearly 70 percent of the squirrels with adequate records were never trapped outside of areas 150 yards in greatest length, although some were occasionally taken several hundred yards from their normal ranges, and others permanently transferred their ranges to different areas. Adult males exhibited the most striking limitation of range, and rarely overlapped with one another. Limited figures gave an average home range of 0.36 acre for adult males and 0.59 acre for adult females. The greatest recorded movement was about 1300 yards; movements appeared to be largely exploratory. Adult squirrels had largely moved by the end of July, but young squirrels moved most often in August and September; young males displayed the greatest tendency to move. Movements appeared to be away from areas of higher density towards those of lower density.

8. Adult males appeared to be more aggressive than other squirrels, and many had visible scars on their heads or bodies. Adult males may possibly maintain individual territories, which they defend against invasion by other males.

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GENERAL NOTES

NOTES ON THE LONG-TAILED SHREWS IN MINNESOTA

Trapping of small mammals, during November, 1940, to August, 1941, has produced some rather interesting if not unusual results concerning the long-tailed shrews of Minnesota. Among these, the high populations of *Sorex cinereus cinereus* Kerr and the extreme scarcity of *Microsorex hoyi hoyi* Baird are the most striking. In addition, some information concerning *Sorex arcticus laricorum* Jackson and *Sorex palustris palustris* Richardson was obtained.

Sorex cinereus cinereus Kerr.—A total of 112 specimens of this species was taken and it was found in all the areas trapped except Martin County (Table 1). This figure seems

TABLE 1. *Summary by species of long-tailed shrews caught*

DATE	LOCALITY	TRAP NIGHTS*	SOREX CINEREUS	SOREX ARCTICUS	SOREX PALUSTRIS	MICROSOREX HOYI
1940						
Nov. 3	Fairmont, Martin Co.	79				
Dec. 17–27	Fairmont, Martin Co.	921				
1941						
Jan. 25	Cedar Creek Bog, Anoka Co.	64				
Feb. 1	Cedar Creek Bog, Anoka Co.	174	1			
Feb. 8	Cedar Creek Bog, Anoka Co.	167	9			
Feb. 15	Cedar Creek Bog, Anoka Co.	150	1			
April 2–May 30	Forest Experiment Station, Carlton Co.	7254	63	6		
June 19–26	Anoka Sandplain, Anoka Co.	945	1			
July 31–Aug. 26	Itasca Park, Clearwater Co.	3120	37	1	1	1
Total		12,874	112	7	1	1

* Small snap back traps were used except in Itasca Park where live traps similar to those devised by Dr. W. H. Burt were employed.

unusually high, especially when it is noted that it ranked second only to the red-backed mouse *Clethrionomys* (118) in total numbers caught and was taken more often than *Peromyscus* (106) and *Microtus* (81). Also, it was found that this species prefers a semi-aquatic habitat, especially coniferous swamps and marshy areas along streams and lakes where there is an abundance of sedges and grasses. The animal is not restricted to these two habitats, however, for it is occasionally found in the more mesic uplands. Indeed, one was taken on the Anoka Sandplain, which is a rather xeric habitat that supports, for the most part, oaks and prairie vegetation. Blowouts on the sandplain, which create temporary bodies of water, probably are responsible for the invasion of such a habitat by this small mammal. The uplands referred to are those bordering swamps and it was found that the cinereous shrew seldom penetrates far into the interior but, for the most part, is restricted to the periphery. In these transition zones, its range was found to overlap that of the white-footed mouse *Peromyscus*, which is seldom caught in swamps. In the coniferous swamp, this shrew is most commonly associated with the red-backed mouse, while in the marshy areas the jumping mouse *Zapus* and the meadow mouse *Microtus* replace the red-backed mouse.

This tiny mammal is active during the day as well as at night for it has been taken during daylight hours. It is to be noted, however, that it seems to be more active on cloudy days than when the sun shines. In addition, it was found to be one of the most active of small mammals during the winter; nor is this activity restricted to runways under the snow for it is commonly caught in traps set on top.

Microsorex hoyi hoyi Baird.—As is to be expected, this shrew proved to be rare or elusive, as only one specimen was taken. Obviously, no conclusions can be reached concerning the habitat preference of this species. The one was taken, however, in a marshy area adjacent to a small stream in Itasca Park where *Sorex cinereus* was common, suggesting that its habits are similar.

Sorex arcticus laricorum Jackson.—Only seven shrews of this species were taken (Table 1). In addition, one specimen was obtained from F. F. Hooper who caught it at Cedar Creek Bog, September 30, 1940. The specimens taken were found in the same areas where *Sorex cinereus* is common (four in marshy areas along streams, three in coniferous swamps). This, of course, indicates that this shrew also prefers semi-aquatic habitats. In fact, one of the animals taken was caught in a trap set on a small elevation that was surrounded on all sides by an inch or so of water. This, to be sure, indicates that this mammal is quite aquatic; more so perhaps, than is commonly suspected.

Conclusions.—The most common shrew in Minnesota during the period November, 1940, to August, 1941, as indicated by trap records, was *Sorex cinereus* (112 taken). *Microsorex hoyi* proved to be rare; only one was caught. *Sorex arcticus*, was also a somewhat uncommon shrew (7 caught). The two favored habitats of long-tailed shrews in Minnesota are coniferous swamps and marshy areas along streams.—Don Quimby, *Division of Entomology and Economic Zoology, University of Minnesota, St. Paul, Minnesota.*

SPEED OF SOME WILD MAMMALS

In the constant struggle of prey to evade predators, Nature has placed a premium on running speed and alertness. That these have had high survival value in the evolution of mammals, there can be little doubt. Even a casual study shows that there is a vast individual variation even among members of the same species and, as would be expected, a tremendous difference exists in the running speed of different species. Conditions of the individual and of the terrain greatly modify the running speed.

Extended field work afforded the writers opportunity to make observations in the field on the running speed of a number of species that seem worthy of recording. Additional records were obtained from refuge superintendents and collaborators. All records given were obtained from the speedometer of an automobile and most records were checked by two or more observers in the car at the time the test was made.—Clarence Cottam and C. S. Williams, U. S. Fish and Wildlife Service, Washington, D.C.

RABBIT MORTALITY ALONG AN IDAHO HIGHWAY

Records of rabbit mortality along U. S. highway 30 through southern Idaho have been published by several observers. Counts were all made during summer or early in the fall and are roughly comparable. During a trip over this road on August 11, 1940, the writer took advantage of the opportunity to make additional observations.

Gordon (1932) counted rabbit carcasses (across Idaho) during the summers of 1929 and 1931. He refers to his route as "highway No. 40" but U. S. 40 does not touch Idaho at any point, and reference to localities mentioned shows that the route followed was actually U. S. 30. He made no count through cultivated areas. In 1929, Gordon's average was slightly over 2 carcasses a mile, but in 1931 it was 8–12 a mile. Along short stretches, some averages were 10 a mile, but in 1931, near Thousand Springs, nearly 100 carcasses a mile were seen over a 2–3 mile stretch. Only one stretch averaged as low as 2 a mile in 1931.

TABLE 1.—*Running speed of mammals*

MAMMAL	MILES PER HOUR	PLACE	DATE	DISTANCE COVERED	REMARKS
Coyote	31	Near Sheldon Refuge, California	7/ 1/41	50 yds.	Probably not quite mature; in front of car; pressed.
Citellus oregonus	8	Malheur Refuge Oregon	6/29/41	50 ft.	On road in front of car. Being pressed.
Citellus oregonus	4-5	Malheur Refuge Oregon	6/29/41	30 ft.	On road in front of car. Being pressed.
Eutamias minimus	10	Malheur Refuge Oregon	6/29/41	50 yds.	On road in front of car. Being pressed.
Porcupine	2	Malheur Refuge Oregon	6/28/41	75 yds.	On dike road between two impounded lakes. Pressed to maximum with aid of switch. To avoid further efforts the "porky" deliberately "fell" into one of the lakes and swam away with about as much speed as he was able to exhibit on land.
White-tailed Jack Rabbit	34	Bowdoin Refuge Montana	7/25/41	50 yds.	In front of car on road.
Black-tailed Jack Rabbit	18	Malheur Refuge Oregon	6/28/41	75 yds.	On road in front of car; not full speed.
Black-tailed Jack Rabbit	27	Malheur Refuge Oregon	6/28/41	300 yds.	On dike road between lake and 18 ft. wide barrow pit. In front of car and pressed to maximum but rabbit left road and jumped into barrow pit and swam by paddling alternately, resembling that of a dog.
Black-tailed Jack Rabbit	28	Malheur Refuge Oregon	6/29/41	50 yds.	On dike road; pressed.
Black-tailed Jack Rabbit	30	Malheur Refuge Oregon	6/29/41	100 yds.	On dike road; pressed.
Black-tailed Jack Rabbit	38	Malheur Refuge Oregon	6/29/41	100 yds.	On dike road; pressed.
Black-tailed Jack Rabbit	38	Malheur Refuge Oregon	6/29/41	100 yds.	On dike road; pressed.
Elk	45 (Maximum for short distance only)	Niobrara Refuge Nebraska	Winter/32	150 yds.	3 year old cow. A report from Refuge Supt. G. A. Amundson. The speed was attained only for a short distance on a flat smooth prairie.
Deer	25	Malheur Refuge Oregon	6/28/41	100 yds.	Running in dense growth of weeds and shrubbery, parallel to car.
Deer	25	Malheur Refuge Oregon	5/-/41	200 yds.	On dike between two ponds. Report by Dr. Clarence Sooter of the Service staff.
Moose	35	Red Rock Refuge Montana	10/-/41	½ mile	Running parallel to drift fence. Report of Supt. Archie V. Hull.
Antelope	32	Sheldon Refuge California	7/ 1/41	½ mile	Two males running parallel with car on very rough lava flow with boulders and brush. Apparently not maximum speed.
Antelope	45	Sheldon Refuge California	4/-/41	—	Parallel with car, near maximum speed. Report from Supt. Sans. He reports a number of speed tests at about 45 miles an hour on fairly level smooth ground.
Buffalo	30	Niobrara Refuge Nebraska	Winter/32	150 yds.	3 year old bull on level ground. Report from Supt. Amundson. Older and younger animals are slower.
Desert Bighorn	30	Aguila Refuge Arizona	Summer/40	½ mile	Ran parallel to a fence at maximum speed on fairly level ground. Report by T. B. Atkins.

Sperry (1933) traveled over much the same route in September 1932 and then counted an average of 2.7 rabbit carcasses a mile over about 275 miles. An average of 1.1 carcasses a mile was seen over 685 miles of Idaho highways, including travel over U. S. 30. Figures for Thousand Springs are not specifically given, but are included in an 80-mile strip that averaged 1.5 carcasses a mile. The highest average count over a short distance was 14 carcasses a mile along a 15-mile stretch.

Williams and Nelson (1939) made counts of dead rabbits along U. S. 30 on August 10–11 and again on August 13–14, 1938. Figures are given for 364 miles of the earlier trip and for 194 miles of the later one. Only 157 miles of these distances can be compared for the two trips. The first trip revealed an average of 6.8 carcasses a mile, while the second trip showed only 5.1 along the same part of the road. The entire 342-mile trip revealed an average of 3.5 carcasses a mile as compared with 5.9 on the 194-mile trip. The Thousand Springs section was one of high counts, averaging 12.0 carcasses a mile on the earlier trip and 19.7 on the later one.

TABLE 1.—*Rabbit Mortality Along U. S. 30 in Idaho, as Recorded by Various Observers, 1929–1940*

OBSERVER	CENSUS DATE	TOTAL DISTANCE US 30 AND 30S	NUMBER CARCASSES SEEN A MILE		
			Average for total mileage	Average for Thousand Springs	Average for short distance
Gordon	"summer 1929"	"across Idaho"	2	—	10 (no mileage)
Gordon	"summer 1931"	"across Idaho"	8–12?	100.0 (2–3 mi.)	100 (2–3 mi.)
Sperry	September 1932	275 miles	2.7	1.5 (80 mi.)	14.1 (15 mi.)
Williams	Aug. 10–11, 1938	364 miles	3.5	12.0 (22 mi.)	13.0 (18 mi.)
Williams	Aug. 13–14, 1938	194 miles	5.9	19.7 (22 mi.)	19.7 (22 mi.)
Smith	August 11, 1940	300 miles	1.7	0.3 (25 mi.)	14.2 (25 mi.)

This writer's records were made in 25-mile units along U. S. 30 beginning at Tremonton, Utah, and ending at Boise, Idaho. Only one of the twelve units included in this journey failed to contain a rabbit carcass, while one had 355 dead rabbits. In the 25-mile unit that included Thousand Springs, the average count to the mile was only 0.3. This same figure was obtained for the unit immediately south of Boise, where Sperry counted an average of 14.1 carcasses a mile over a 15-mile stretch in 1932, and where Williams and Nelson found 2.1 carcasses a mile in 1938.

The accompanying table shows that counts of this kind may vary as much as 60 percent within a four-day period, and that over a period of a year, counts may vary from 0 to 100 a mile along the same area. There seems to be an indication of a comparatively high population in 1931 and 1938, and of a low point during 1929, 1932, and 1940. There is some evidence of a sudden decrease in population during the latter part of 1931 and the early part of 1932 and between 1938–40.

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C. F. SMITH, *Fish and Wildlife Service, Mount Shasta, California.*

A MALFORMATION IN DEER

Following reports by Adam Wilson that a number of deer (*Odocoileus virginianus texanus*) in the divide country around the head of the South Fork of the Guadalupe River, Kerr County, Texas, were found to have a pronounced swelling of the lower jaw, authority was granted by William J. Tucker, executive secretary of the Texas Game, Fish and Oyster Commission, to R. R. Ramsey of the Texas Cooperative Wildlife Research Unit to kill some of the deer for study.

There were field reports of emaciation, in certain instances, in association with the lump-jawed condition, and there was some anxiety over the possible indication of a serious infectious condition such as lump-jaw caused by *Actinomyces bovis* or a disease known as calf diphtheria caused by *Actinomyces necrophorus*. Lump-jaw has been reported in deer and in October 1939 three deer from Kerr County were brought to the A. and M. College infected with *A. necrophorus*. Two of the animals had foot-rot and in one the tissues in the laryngeal region (calf diphtheria) were involved. The infection produced a generalized swelling of the lower jaw.

Two affected deer were killed (one each on October 7 and October 10, 1941), placed on ice at Kerrville, and (on October 16) carried to the School of Veterinary Medicine at the Agricultural and Mechanical College of Texas, College Station, where Van Volkenberg made the examination reported here.

Between the rami of the mandibles a noticeable rounded swelling was found projecting below the natural boundaries of the lower jawbone in each of the two deer. As evidenced by palpation with the fingers, the swellings were of a doughy consistency. Cutting through the skin and subcutaneous tissues surrounding the swelling revealed a compact mass of hair, masticated food, and several whole acorns. In one of the deer the mass was approximately the size of a tennis ball; in the other it was slightly smaller.

The sublingual folds are mucous membranes on each side of the floor of the mouth attached laterally on one side to the tongue and on the other to the medial surface of the ramus of the mandible near the base of the cheek teeth. Exploration disclosed that the part of the left sublingual fold directly below and extending the length of the row of cheek teeth was many times its normal width. The portions of this fold anterior and posterior to the cheek teeth and the entire right sublingual fold of each animal appeared normal. The abnormally wide fold on the left side formed a diverticulum beneath the tongue, with a slit-like opening below the left cheek teeth. Some of the mouth contents had collected and become impacted in the diverticulum. The mass, held down from above by the heavy muscular tongue and laterally by the jawbone pressed against the muscles, fascia, and skin between the rami, had caused these soft tissues to bulge. The resultant external abscess-like swellings were easily visible among affected wild deer on the range.

There was no evidence that the mass underneath the tongue had caused anything more than perhaps some annoyance to the two affected animals. No gross pathological changes, such as might be expected from irritation caused by coarse material in an unnatural location in the body, could be detected either in the sublingual fold or in the adjacent tissues.

It was impossible to determine whether the diverticula found in these two animals were present at birth. Possibly the abnormally wide sublingual folds were congenital as the condition was found in equivalent tissues in two deer from the same region. The deep pockets with the slit-like openings might have developed after birth, thereafter becoming enlarged by the gradual accumulation of impacted food.

A third deer, a male with 10-point antlers, killed in Kerr County during the latter part

of the season, December 1941, was brought to the College January 17, 1942. Conditions observed were essentially the same as in the others, except that the opening into the ventral diverticulum was on the right rather than on the left side of the tongue. There was some hair in the pocket under the jaws, a few oak leaves, some miscellaneous unidentified food material, and about a dozen whole acorns. Also present were a number of worms (larvae of some lepidopterous insect).

Examination of these specimens indicate that there is no cause for concern regarding this particular type of lump-jawed condition observed in certain deer in Kerr County, Texas.—H. L. Van Volkenberg, *Dept. Veterinary Parasitology*, and W. P. Taylor, *Texas Cooperative Wildlife Research Unit, College Station, Texas.*

NOTES ON THE ROOSTING-PLACE OF PIPISTRELLUS HESPERUS

The little western canyon bat (*Pipistrellus h. hesperus*) has generally been considered strictly a crevice dweller, roosting under slab rock and in crevices of cliffs. Very few specimens are on record that have been collected alive from their roost, with most specimens being obtained by shooting them as they forage through the air before dusk. Von Bloeker (Jour. Mamm. vol. 13, no. 3, p. 273, 1932) records three specimens captured alive from under loose rocks, while Burt (Trans. San Diego Soc. Nat. Hist., vol. 7, no. 36, p. 396, 1934) tells of taking one from a small crevice on the side of a cliff in southern Nevada.

In view of the scanty information on the actual capture of this common bat in its diurnal roost, it seems worth while to record further instances of live capture and to comment on a type of roosting place heretofore unmentioned in the literature dealing with this species.

On July 20, 1935, while engaged in some extensive bat collecting in the Riverside Mountains, Riverside County, California, I took a lactating adult female *Pipistrellus h. hesperus* from a pocket in the rock wall forty feet from the entrance of a 150 foot mine tunnel. The bat was resting on top of a horizontal surface and not suspended head downward. No trace of her young could be found.

On the morning of August 4, 1935, at the same locality I prepared to enter a tunnel similar to the preceding one, but found my way blocked by two large and decidedly hostile rattlesnakes. While busily engaged in dispatching the two snakes, I startled the bat population of the tunnel into flight. A total of seven bats were roosting in the short tunnel and as they passed out into the sunshine they were easily identified as *Pipistrellus h. hesperus*. Instead of scattering and seeking new roosts, the seven bats flew leisurely about the entrance and then returned to the darkness of the tunnel. This occurred several times with the pipistrelles being within ten feet of me on numerous occasions, thus making identification positive. After successfully removing the rattlesnakes which had blocked my path, I entered the tunnel and managed to collect two of them. The other five again flew out of the tunnel, but did not return.

A third instance of the occurrence of *Pipistrellus h. hesperus* in a cavernous type of roost came to my attention on August 19, 1937, while I was collecting bats eight miles north of Parker, Yuma County, Arizona. On this occasion I entered a large, high-roofed mine tunnel. This particular tunnel followed an ore vein and the high ceiling was due to the miners' efforts to take out as much of the ore as possible. The walls and celing were decidedly rough, with many shelves and large pockets, as compared to the relatively smooth walls of an ordinary type tunnel. A short distance within the tunnel a large colony of *Macrotus californicus* was discovered and when disturbed, beat a rapid retreat to a point deeper within the mine. Upon the departure of the leaf-nosed bats, several small bats were observed circling overhead. With the aid of a large mouthed hand net, several of them were captured while in flight, and upon examination proved to be *Pipistrellus h. hesperus*. They were observed alighting on small ledges near the ceiling or crawling into rock crevices. Reaching the ceiling on some make-shift scaffolding, I succeeded in securing several more specimens of this species with the aid of long-nosed scissor forceps which permitted extraction of the tiny bats from deep crevices. In every case, however, pipistrelles were roosting singly. Eleven specimens were taken from this roost, four of them being females.

In conclusion it may be said that although *Pipistrellus h. hesperus* generally roosts in rock

crevices and under loose rock on hillsides; it will, however, when conditions are right, select a cavernous type of roost if the particular mine tunnel or cave is to its liking. It might be well to point out at this time that all three of these observations were made during the hot summer months and whether the pipistrelles inhabit the same mine tunnels during the winter months remains to be determined.—KENNETH E. STAGER, *Los Angeles Museum, Los Angeles, California.*

A RECORD OF ZAPUS HUDSONIUS IN NORTHEASTERN OHIO

According to Trautman (List of the Mammals of Ohio. Ohio Division of Conservation Bulletin No. 54, 1931), *Zapus hudsonius hudsonius* (Zimmerman) is rare throughout the state. Katz (A Key to the Mammals of Ohio. Ohio Wildlife Research Station, Release No. 158, 1941) states that this species may often be found locally in certain northern parts of the state. The writer, while conducting a field trip with a class in ecology, found and captured a specimen of this species in October 1937 in a steep and narrow river gorge cut through sandstone at Stow, Ohio. This gorge now serves only for the drainage of several small springs and for run-off during periods of heavy precipitation. The floor of the gorge is a floodplain; the slopes have for the most part reached a beech-maple climax, while along the rim are a number of relict hemlocks. The jumping mouse was discovered on the floodplain in the bottom of a shallow, dry well enclosed by a concrete rim 3.5 feet in diameter and 4 feet deep. The mouse was shaking violently, apparently from fright, and was easily captured, not moving or attempting to escape.—RALPH W. DEXTER, *Kent State University, Kent, Ohio.*

BAMBOO AS PANDA FOOD

The New York Zoological Society has recently acquired a pair of giant pandas, the gift of Madame Chiang Kai-shek and Madame H. H. Kung to the people of the United States as a token of the Chinese people's appreciation of the practical expressions of our friendship that have reached them.

Incidental to the arrival of the pandas is the introduction of living plants of a species of bamboo known to constitute an important part of their natural daily diet. The fact that the principal natural diet of the panda is bamboo, of which it may eat as much as 20 pounds of the leaves and twigs in a single day, complicated the problem of providing food for the long, half-way-'round-the-world journey from China to America. Mr. John Tee-Van, the Zoological Society's representative, brought with him from Chungking sufficient bamboo for the first few days of the homeward journey, and when this was exhausted, fresh material of locally available bamboos was secured at Manila, Honolulu, and San Francisco.

From specimens submitted to me by Mr. Tee-Van for identification, and from information imparted by Mr. R. A. Young, Associate Horticulturist, Division of Plant Exploration and Introduction, Bureau of Plant Industry, U. S. Dept. of Agriculture, I am able to report that the following bamboos are known to be palatable to the panda:

1. *Arundinaria tecta* Muhlb. Switch Cane.—Native to our southern states.
2. *Bambusa multiplex* (Lour.) Raeusch. Hedge Bamboo.—Native to Kwangtung, China, and introduced in warm regions throughout the world as a hedge plant and potted ornamental.
3. *Dendrocalamus strictus* (Roxb.) Nees. Native to India.
4. *Sinobambusa tootsik* (Mak.) Makino. Native to China; introduced in the Hawaiian Islands and continental United States.
5. *Phyllostachys sp.* A Chinese bamboo in cultivation at Chengtu, Szechuan, China.
6. *Pseudosasa japonica* (S. & Z.) Mak. (*Arundinaria japonica* S. & Z.) Metake. A Japanese bamboo widely disseminated in cultivation. The commonest species in cultivation in colder parts of the United States, it thrives in the vicinity of New York, and is known to survive out of doors on our eastern coast as far north as Boston.
7. *Sasa senanensis* (Franch. & Sav.) Rehder. A large-leaved Japanese bamboo of low stature, material of which was supplied by the Arnold Arboretum. According to Dr.

Donald Wyman, clumps in the open ground at the Arboretum often come through the winter with little or no injury from cold.

8. *Sasa chrysantha* (Mitf.) E. G. Camus (*Arundinaria chrysantha* Mitf.). A small Japanese bamboo.

9. *Sinarundinaria sp.* Native to the haunts of the panda at altitudes between 6000 and 9000 ft. in the mountains of Szechuan, China.

Mr. Tee-Van brought with him to the United States living plants of nos. 5 and 9 in the foregoing list for propagation by the Division of Plant Exploration and Introduction. These are now being grown under quarantine, and it is hoped that they may later be successfully introduced into cultivation, for they will delight the eye of man as well as tickle the palate of the panda. Meanwhile, existing supplies of *Pseudosasa japonica* (no. 6 in the foregoing list) of which new local sources are being reported at a gratifying rate, bid fair to be adequate and satisfactory for the pandas' current need.

It is noteworthy that the panda, which is considered to be rather exacting in its food habits, will eat, with apparent relish, fodder from as many as nine species of bamboo representing eight different genera. There seems to be some disagreement, however, between different reports as to what part of the bamboo is eaten. All agree that the fresh leaves, twigs, and young shoots are readily accepted. Especially is doubt cast upon reports that the fodder will sometimes be eaten after it has become dry, and that well-hardened culms up to a half-inch in diameter may be eaten by the panda. Mr. Tee-Van has the following to say on these points:

"The two New York pandas on their journey from China refused to eat dried bamboo stalks or leaves, and at the Zoological Park they continue to exercise that discrimination. During part of the long steamer journey when the refrigerated cut bamboo had dried up, leaves of bamboo were cut into pieces half an inch long, soaked in water for half an hour, the excess water drained from the leaves, and the cut leaves then mixed with the pandas' boiled cornmeal mush, to which honey, milk and sugar had been added. The pandas eagerly accepted this mixture.

"As to eating well-hardened culms up to half-inch in diameter, the supposed male of the New York pair, an animal 60 lbs. in weight in November and 90 lbs. in weight on March 1st, has devoured stems up to 4 mm. in diameter. There was general agreement among people in China who had known pandas that larger animals can devour culms up to one-half inch in diameter."—F. A. McClure, *Division of Plant Exploration and Introduction, Bureau of Plant Industry, U. S. Dept. of Agriculture, Washington, D. C.*

FISHER ABROAD IN DAYLIGHT

While on duty near the base of the General Sherman Tree at 2:10 p.m. on August 5, 1941, my attention was called to a cat-like animal that was moving through the forest about 75 yards distant. The outline at first caused me to believe it to be a marten, but a glimpse of the long tail convinced me that it was a fisher (*Martes pennanti*). The mammal moved in a leisurely manner and I pursued it as quietly as possible. When it stopped, I did likewise, using whatever cover was available. I am reasonably certain that the fisher saw me, but it showed no apparent concern. After going some 50 yards, with about three stops to look about, the mustelid jumped deftly onto a fallen log about four feet in diameter and disappeared on the opposite side. I went to the log as quickly as possible, and climbed upon it. The fisher was not in sight.

In about one-half minute it appeared from behind a large fallen branch some 15 feet from me and looked toward the west, downhill. Suddenly the animal turned and came directly toward me, passing through a large break in the log, almost beneath my feet. I was about five feet above the fisher, but apparently it neither saw nor smelled me. After passing under the log, it went about ten feet before stopping and sniffing the air. From the log I had an excellent view of the dark body and the lighter cinnamon-colored hairs across the shoulders, the "belligerent" (to us a human description) expression on the face, and the long tail, which seemed out of proportion to the rest of the body. The fisher paused about 30 seconds, sniffing the air in a seemingly-unconcerned manner. Suddenly it seemed to get

my scent (I was only about ten feet away) because it moved rapidly toward the Sherman Tree. Again I pursued, but was greatly outdistanced. The fisher crossed the fenced-off area around the tree, and when last seen it was moving up the hill above the Wolverton road at a fairly rapid rate. This is the only sight record of the fisher in this vicinity in recent years of which I have been able to learn.—Douglass H. Hubbard, *Sequoia National Park, California.*

GRAY FOX DEN IN DISCARDED MILK CAN

Although the gray fox (*Urocyon cinereoargenteus*) is known to den in a variety of situations, the following record seems worthy of note.

In late May, 1940, a farmer in Beaver County, Pennsylvania (1 mile west of East Palestine, Ohio) discovered a gray fox den in an old 10-gallon milk can. The can had been piled, along with rubbish and discarded farm machinery, some time before in a ravine 50 feet from the back of the farm buildings. Several times an adult fox had been observed leaving the vicinity of the den. Upon investigation the milk can was found to contain four young gray foxes the size of half-grown house cats. The nest consisted of a thin layer of leaves and grass. How long the foxes had occupied this den is not definitely known.—Hubert Bezdek, *Ohio Division of Conservation, Columbus, Ohio.*

NOTES ON SOME BATS OF THE SOUTHWEST

The bats listed here were secured in several localities in the southwestern part of the United States, and are now deposited in the Zoology Museum of the University of Utah.

Mormoops megalophylla senicula Rehn.—One specimen was taken in Edinburg, Texas, in February 1934 and two in January 1935. Only one other specimen of this bat is known for the United States.

Lasiurus cinereus cinereus Beauvois.—A large specimen of this winter migrant was taken in Edinburg, Texas, on January 24, 1936.

Lasiurus borealis borealis Muller.—A single specimen was taken from the vestibule of the Edinburg Junior College Science building in 1936. Three others were found hanging among the leafy branches of a pecan tree 16 miles south of Kerrville, Texas, in July 1940.

Nycticeius humeralis humeralis (Rafinesque).—A single specimen was taken near Edinburg, Texas, in 1935.

Antrozous pallidus pallidus (LeConte).—Five specimens were taken 16 miles south of Kerrville, Texas, in August 1939. These came from a mass of about fifty that had settled under the eaves of a ranch house.

Myotis thysanoides thysanoides Miller.—A single specimen was taken near Mayhill, New Mexico, on August 19, 1935.

Tadarida mexicana mexicana (Saussure).—This species is common over most of southwestern Texas. A number of specimens were taken at Edinburg, Texas.—Stanley Mulaik, *Department of Biology, University of Utah, Salt Lake City, Utah.*

ZONAL DISTRIBUTION OF THE CALIFORNIA MASTIFF BAT

For the past six years the writer has studied and collected bats from the region in and about Barrett Dam, San Diego Co., California. During this time he and Richard Neil collected a large series of *Eumops perotis californicus* (Merriam) one and one-half miles north of Barrett Junction. In looking up material on the range of the *Eumops* the writer discovered that heretofor it had been reported only from the Lower Sonoran Zone (see H. W. Grinnell, *A Synopsis of the Bats of California*, 1918 and Grinnell, *Recent Mammal Fauna of California*, 1933). The following plant indicators of the Upper Sonoran Zone occur in and about our bat collection region: *Yucca Whipplei, Quercus agrifolia, Adenostoma fasciculatum,* and *Ceanothus divaricatus.*

Due to the fact that the California Mastiff Bat is definitely established in this region, it is thought advisable at this time to record the zonal range of *Eumops perotis californicus* as including the Upper Sonoran Zone in the San Diegan Region.—Philip H. Krutzsch, *San Diego State College, San Diego, California.*

ALTITUDINAL RECORD FOR THE SPOTTED SKUNK IN CALIFORNIA

On November 25, 1941, the writer captured a spotted skunk (*Spilogale gracilis saxatalis*) at an altitude of 8,400 feet, two and one-quarter miles west of the Sonora Pass, Tuolumne County, California. This, so far as known, constitutes an altitudinal record exceeding by over 2,000 feet any previously reported for this species. The habitat in which this individual was secured was unusual in that it was zonally far above that normally occupied by spotted skunks, being well up in the Canadian Life Zone. Red fir (*Abies magnifica*), white pine (*Pinus monticola*) and lodgepole pine (*Pinus contorta* var. *murryana*) were the dominant trees in this locality, which was the granitic canyon of the upper part of the Middle Fork of the Stanislaus River. The area was inhabited by boreal species of mammals such as golden mantled ground squirrels, red squirrels, flying squirrels, and pine marten, all of which had either been observed or secured within 100 yards of where the spotted skunk was taken. The latter animal was caught in a steel set placed for pine marten and tracks of marten at the time were in evidence on the snow which covered the ground to a depth of four inches.

It appears probable that this skunk, an immature female, slightly less than two-thirds grown, had wandered west from the east side of the Sonora Pass where Great Basin environmental conditions prevail. Lateral stripes are lacking on this specimen as is generally true of the race *saxatalis* occupying the northern Great Basin region.—ROBERT T. ORR, *California Academy of Sciences, San Francisco, California.*

FIVE KITTENS WITH CONJOINED UMBILICAL CORDS

In a litter of eight kittens born to an orange-yellow "alley cat" in June 1941 near Stillwater, Oklahoma, five had their umbilical cords united distally and appeared to have been

PLATE 1

Kittens born united by their umbilical cords. Photographed after being preserved as a museum specimen. Note the deformed condition of the hind limbs of the detached individual.

attached to a common placenta; the placenta, however, was not observed. When the five specimens were received, as a gift to "Science" from Mr. Fred Gilman, four of them were alive, still connected, and of apparently normal structure in the body proper. The fifth individual was dead, its cord was broken, and its hind limbs were seriously deformed as a result of having been entangled *in utero* with the cords. The animals were sexed by dissection—two males, three females. The females are tricolored (black-, yellow-, and white-spotted), the males allover yellow.

The authors have indulged in considerable speculative discussion concerning the embryological and genetic aspects of this case. The variations in sex and color militate strongly against the view that the animals may be identical quintuplets. Furthermore, it would seem that even identical offspring should have separate placentae. Nevertheless, it is conceivable, although perhaps very highly improbable, that the five siblings did derive from a single zygote and that a part of them underwent sex reversal with concomitant sex-controlled change in coloration.—R. O. WHITENTON, H. W. ORR, R. N. DANIELSON, AND R. C. HUGHES, *Departments of Physiology and Zoology, Oklahoma Agricultural and Mechanical College, Stillwater, Oklahoma.*

THE POCKET GOPHER IN RELATION TO YELLOW PINE REPRODUCTION

In connection with a pocket gopher-mountain meadow range study started in 1931 on the Ochoco National Forest in Oregon, an interesting condition appeared concerning the reproduction of yellow pine (*Pinus ponderosa*).

Interspersed throughout the forests are openings or meadows, the forage of which is utilized primarily by sheep and cattle on an allotment and rental basis. The accompanying table shows the result of an inventory made in September 1940.

This forest is in that area known as the Blue Mountains and over which as a whole pine reproduction is more dense than is desirable for satisfactory timber growth. Also from the viewpoint of those interested in wildlife and livestock no desire is evident to reforest the existing natural openings.

TABLE 1.—*Yellow pine seedlings counted on plots*

		PAIRED PLOT[1] NUMBERS					
		1	2	3	4	5	Totals
Pocket Gophers Removed	Stock Exclosure	19	112		566		697
	Grazed Control	0	0		0		0
Pocket Gophers Unmolested	Stock Exclosure			0		7[2]	7
	Grazed Control			0		0	0

[1] Plots ¼ acre in size except No. 2 exclosure which contained ½ acre.

[2] Current season seedlings in one spot as result of a mouse cache.

The table indicates that grazing and the presence of pocket gophers (*Thomomys talpoides quadratus*) are responsible for the lack of reproduction on the plots. When pressed for food, livestock will consume most growing green vegetation within reach and as the plots were subjected occasionally to the demands of bunched bands of sheep the reason for lack of reproduction on the unfenced controls is apparent.

Food of the pocket gopher probably embraces as wide a variety of vegetation as that of any animal and includes the roots, tops and bark of those pines occuring in its range. No

indication, however, has been found that the animal consumes naturally disseminated pine seed and while captive pocket gophers taken from this study area partook readily of other food, pine seeds were rejected.

Utilization of pocket gopher runways by white-footed mice (*Peromyscus spp.*) is the primary cause of the lack of reproduction within these exclosures inhabited by the gophers. This is shown by pine seed hulls found within the burrows and in the dirt of the mounds thrown up when abandoned runways are reoccupied by the pocket gopher. The areas from which these burrowers have been removed and the tunnels have collapsed do not afford the mouse shelter and as a result the seeds are gleaned less thoroughly by the seed eating rodents.—A. W. Moore, *Fish and Wildlife Service, Hillsboro, Oregon.*

NOTES ON MANATEES IN FLORIDA WATERS

During the cold spell of January, 1940, a number of manatees, *Trichechus manatus latirostris*, succumbed and their bodies were washed ashore and stranded by the tide at various points in the vicinity of Charlotte Harbor on the west coast of Florida. Cahn (1940) stated that four dead manatees were found at the mouth of the Peace River which empties into Charlotte Harbor near Punta Gorda, and a fifth was found dead just south of the mouth of the Caloosahatchee River near Fort Myers. Gunter (1942) mentioned the death of one manatee in the Peace River near Cleveland, Florida, and four others that were killed at the same time in the Peace River, the bodies of which were found in Charlotte Harbor. It may be that these men made reference to the same animals. Gunter (1941) made the statement. . . . "It is well known that manatees are very susceptible to cold. . . . The extremely severe cold wave of the past winter (January, 1940), probably would have killed any manatee on the northern Gulf Coast." . . . Although manatees have little need for insulation under usual tropical conditions, they are well supplied with fat and a heavy skin covering. This is, however, inefficient in insulating the body against unusual lowering of the air temperature. Howell (1930) suggested that the connection between the capillaries of the oil system and the vascular capillaries in the cetaceans might be sufficiently close to allow for a possible interchange of carbon dioxide by diffusion. This possibility might also be applicable to the tropical sirenians and might explain the abundance of fat and oil as an absorptive mechanism for excess carbon dioxide.

On June 2, 1940, while assisting Dr. C. M. Breder, Jr. at the Florida laboratory of the New York Aquarium, the writer collected a complete manatee skeleton on the eastern shore of La Costa Island. The skin of the animal was still fairly intact at the time, although the fleshy parts were almost completely decomposed. The skeleton is now in the Museum of Zoology of the University of Illinois. Mr. Robert Spearing, local guide for the laboratory staff, told of three other manatee bodies that had been stranded near South Boca Grande. These bodies had been buried by the local people.

More important than the observations on dead manatees, was the finding of five living manatees by Mr. Spearing and the writer on June 30, 1940. While returning from a collecting trip, we sighted the five animals feeding on eelgrass along the outer shore of Sanibel Island about two miles below Blind Pass. When first seen the animals were in about five feet of water. During 45 minutes observation, we distinguished what appeared to be one bull, about 12 feet in length, three cows about 9–10 feet in length, and one calf about 3½ feet in length. At first the bull reared part way out of the water and headed out toward the open Gulf of Mexico, closely followed by two of the cows. The other cow, apparently the mother of the calf, started southward along the shore accompanied by her offspring. From his actions, it appeared that the bull was trying to divert our attention from the cow and calf although while we were in the vicinity he did not move more than a quarter-mile from them.

In a recent communication from Dr. Breder, he mentioned that, as of June 1942, Mr. Spearing has seen no manatees since the above-mentioned observation.

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LOUIS A. KRUMHOLZ.—*Institute for Fisheries Research, Michigan Department of Conservation, Ann Arbor, Michigan.*

GESTATION PERIOD IN MEARNS COTTONTAIL

Late in the afternoon, Feb. 19, 1937, a pair of penned Mearns cottontails, *Sylvilagus floridanus mearnsii* (Allen), in copulation were observed by Henry H. Schwane, one of several students assigned to observations. The female prepared a nest entirely of hair on the frozen soil surface in a small shelter of lumber and bricks, and bore five young at night late on March 17, or early on March 18. The gestation period then was approximately 26.5 days. Dice (Jour. Mamm. vol. 10, pp. 225–229; vol. 14, p. 162) reported the probable gestation period for the Oklahoma cottontail, *Sylvilagus floridanus alacer* (Bangs), as 28 days, or less. Gerstell (Pa. Game News vol. 8, no. 2, pp. 8–10, 32) stated that cottontail births occurred at any time between 25 and 32 days after copulation, the normal period of gestation apparently being 30 days.—GEORGE O. HENDRICKSON, *Dept. of Zoology and Entomology, Iowa State College, Ames, Iowa.*

EASTERN CHIPMUNK IN NEBRASKA

On November 15, 1937, an unidentified trapper gave me an adult female eastern chipmunk (*Tamias striatus*) that had caught itself in a snare originally set for rabbits. This animal was taken in the Fontinelle Forest Reserve north of Mill Hollow. I subsequently mounted the specimen, which is still in my collection.

To my knowledge the specimen I have in my collection is the only eastern chipmunk preserved from Nebraska.—RALPH VELICH, *Department of Zoology, Lincoln, Nebraska.*

REVIEWS

Mayr, Ernst. SYSTEMATICS AND THE ORIGIN OF SPECIES. Columbia University Press, 334 pp., 29 figs. $4.00.

Considerable interest in the processes of speciation has developed in the past few years and several comprehensive treatises on the subject have appeared in print. Those by Rensch (Proc. Linn. Soc. London, 150th Sess., pp. 275–285, 1938), Huxley, *et al.* (The New Systematics, 1940), Dobzhansky (Genetics and the Origin of Species, 1941), and the several symposia on species and speciation are among the more important contributions. The present work complements, in a fashion, that of other authors as it is written from the view point of a systematist whose principal field has been Ornithology.

To Linnean naturalists, the species was a static, rigid entity, arising by special creation or saltation. This concept was materially altered by the researches of Darwin and Wallace, who emphasized the origin of species by the processes of accumulation of small mutations, accompanied by geographic isolation, and was further altered by Rossmassler (1836), Kobelt (1881), Sarasin (1899), and Gulick (1905) in the concept of the polytypic species composed of two or more geographically complementary and varying races or subspecies. To this concept, further refined by Rensch and numerous American students, particularly in the fields of Ornithology, Mammalogy, Conchology, and Entomology, the author devotes most of his attention.

According to the author, "a species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers."

The reviewer is in full accord with this concept, as are many other students of speciation, but many "conservative" systematists, at least in Mammalogy, insist on actual, demonstrated intergradation before they feel justified in uniting two or more closely similar "species" (populations) under one specific name. This procedure has some justification in that it counters the tendency of "lumpers," but, basically, it is without foundation in most instances, at least in Mammalogy, and, as Mayr illustrates clearly, in Ornithology.

To illustrate the height of "conservatism," Merriam (N. A. Fauna, 41, 1918) recognizes six polytypic species (one with three geographic races, five with two) and fifty-five "full" species of grizzly bear in North America. This treatment of a large carnivore that has a home range of several miles in radius not only is absurd, but it so obscures the actual relationships of the group that further work must be done to clarify their now chaotic systematic status. The reviewer ventures the opinion that *all* these "species" of grizzly freely interbreed in nature where their ranges are in contact, or that they are potentially capable of doing so in instances of geographic isolation. If one accepts Mayr's definition of a species, it will likely be necessary to reduce these 61 "species" to a single polytypic species with possibly three or four geographic races.

Instances such as that cited not only justify Mayr's criticism of mammalian taxonomists, but they also obscure relationships and lead to confusion and bewilderment. Happily, the reviewer can state that the present tendency in Mammalogy is definitely toward the concept of polytypic species. Osgood, in his treatment of *Peromyscus* in 1909, definitely had this concept in mind, and practically all of the recent systematic papers in Mammalogy deal with polytypic species.

No mammalogist who has any interest whatsoever in the problems of distribution, differentiation, and speciation can afford to overlook this contribution. To the reviewer, it ranks with such contributions as Matthews' "Climate and Evolution."

The book is well printed and has few typographical errors. The author and the publishers deserve praise for a task well done.—W. B. Davis.

Beard, Daniel, *et al.* Fading Trails. The Macmillan Company, 279 pp., illus. $3.00.

To conservationists interested in the present (1942) status of threatened wildlife species, Fading Trails "is a ringing challenge." The book denotes three chapters to primitive conditions and the effects of exploitations by "Civilization's Heavy Heel," followed by the story of decimation of 26 native species.

Of particular interest to mammalogists are the sections on grizzly bear, bighorn, woodland cariban, sea otter, rare fur bearers, manatee, wolf, and mountain lion, each one of which has been decimated by the ruthlessness of man nearly to the point of extinction. Other species treated are: California Condor, Nene (Hawaiian Goose), Trumpeter Swan, Pinnated Grouse, Hudsonian Godwit, Snail Bird (Everglade Kite), Florida Crane, Roseate Spoonbill, Whooper (Whooping Crane), Swallow-tailed Kite, White Hawk, Ivory-billed Woodpecker, Puerto Rican Parrot, Great Lakes Whitefish, Atlantic Salmon, Lobster, Green Turtle, and American Crocodile.

Each one of the threatened species can be perpetuated in some measure by proper management. The U. S. Forest Service, the U. S. Fish and Wildlife Service, and several State agencies have made a good beginning in this direction, but they cannot do the job alone. Every American needs inspiration and encouragement to assist in the task. Fading Trails will certainly enlist the backing of all those who read it.

The book is authentic, well written, and should appeal to every real American.—W. B. Davis.

Dixon, Joseph S. WILDLIFE PORTFOLIO OF THE WESTERN NATIONAL PARKS. U. S. Government Printing Office. $1.25.

Good photographs of wild animals under natural conditions are not commonplace, so the present volume by an outstanding wildlife photographer is indeed welcome.

The portfolio includes 35 pictures of mammals, 15 of birds, and 2 of reptiles, all of which, with few exceptions, were taken by the author himself. "No movie trained animals or other high-pressure methods have been used to procure spectacular results. All of these photographs are of living wild animals in their native habitats." Each photograph is accompanied by a brief account of the animal.

All naturalists should enjoy this contribution, and those who have tried to take similar photographs will appreciate the patience, perseverance, and ingenuity of the author.—W. B. DAVIS.

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COMMENT AND NEWS

LETTER TO THE EDITOR

Sir:

In the issue for August 1942, Gordon Gunter has the following passage in his article on the Bottle-nose Dolphin: "I have seen dolphins overtaken and run over by outboard motor boats that were making 22 miles an hour at the most . . . the 50 mile an hour speed, for which they (the dolphins) are given credit by a popular magazine, is preposterous."

Without defending the estimate of the "popular magazine" I would suggest that it would be a grave error to assume that no member of the cetacea can travel faster than 22 m.p.h. An observer on board a destroyer has informed me that he has seen dolphins (porpoises were actually named but as dolphins are known to be the faster animals I have taken leave to substitute them in the description) zig-zagging in front of the ship when she was making 32 knots. This would indicate a speed for the dolphins in the region of 40 m.p.h.

Such a record does not stand by itself. Other observers on fast ships have recorded similar occurrences. Perhaps the best of these is to be found in Prof. Luis Roule's "Fishes, Their Ways of Life." Roule describes how he was an observer on a torpedo boat sent out to frighten some porpoises off a certain fishing ground in the Mediterranean.

Roule writes: "The torpedo boat was going at full speed and making about 30 knots.

But despite this great speed, the porpoises outdistanced us easily. They turned under the bows and played all sorts of tricks about the ship without seeming the least perturbed."

Roule adds that when the boat opened fire the porpoises dived and did not appear again before the evening. The following night they came back to harry the fishermen's catches. As soon, however, as a torpedo boat came in sight the animals recognized it, took to flight and appeared again only when the boat had gone.—FRANK W. LANE, *Chipperfield, Evelyn Avenue, Ruislip, Middx., England.*

CHEESMAN TRANSFERS

Mr. William H. Cheesman, charter member of A. S. M. has transferred to the Bureau of Plant Industry after twenty-nine years of service with the Fish and Wildlife Service.

DAVIS IN ARMY

Dwight D. Davis, formerly associated with the Field Museum of Natural History is now Pvt. D. D. Davis, 13th General Hospital, Camp Robinson, Arkansas.

GENERAL COUNCIL ON ZOOLOGICAL NOMENCLATURE

The undersigned zoologists, resident in the United States of America, at the invitation of the Committee on Nomenclature of the American Society of Mammalogists and with the cooperation of the "American Commission on Scientific Nomenclature" of the Entomological Society of America, do hereby associate themselves together as a society and certify as follows:

First: The name of the society shall be the General Council on Zoological Nomenclature.

Second: The objects of the Society shall be:

(A) To act in an advisory capacity in all matters concerning zoological nomenclature during the World War and for such time thereafter as it may consider desirable.

(B) To administer, amend, interpret, and maintain a code of nomenclature for the use of zoologists.

(C) To cooperate with societies maintaining committees on nomenclature, at least those represented in its own membership.

(D) To retain within itself important powers of decision and legislation and of substitutions and additions to its membership, but always subject to full hearings and the advice and counsel of one or more of the committees above mentioned.

(E) To cooperate with zoologists practised in nomenclature who are residents of foreign countries when the war is ended or as soon thereafter as may be practicable.

G. F. FERRIS	REMINGTON KELLOGG
WILFRED H. OSGOOD	H. A. PILSBRY
JAMES A. G. REHN	KARL P. SCHMIDT
GEORGE G. SIMPSON	A. WETMORE
JOHN T. ZIMMER	

Merely on the face of it, the above may seem to be a self-constituted body of dubious possibilities and audacious construction. That this is not the case may be evident when its history and purposes are explained. It is the outgrowth of numerous informal discussions among a large number of zoologists during the past few years and of formal action taken by at least two national societies.

Even in years just prior to the war, the International Commission on Zoological Nomenclature was relatively inactive and after hostilities began in Europe in 1939 it became practically nonfunctional. This created a situation in which all cooperative action was endangered and nearly a century's hard earned progress in nomenclature was threatened. Individuals and organizations began to discuss special codes for their separate groups only and in some cases took definite action. Recently a German (Poche) has promulgated a code of his own and in general at the moment every zoologist having a nomenclatural

problem finds himself without appeal to any constituted authority. It was precisely to avoid this condition that codes and commissions were devised.

Discussion among zoologists unanimously recognized the emergency, but it was difficult to arrive at a basis for action which did not involve very great delay and longdrawn controversy. There were those who felt that the international idea could not be abandoned and others who advocated complete divorce from the Old World. The latter pointed to the success of the International Commission as being mainly due to the American C. W. Stiles whose final conclusion (see Science, vol. 73, pp. 349–354, 1931) was that it was not further workable. Among those holding this opinion were several Europeans.

As announced in *Science* (vol. 95, p. 598) the Entomological Society of America, pursuant to action taken at its meeting in December, 1941, formed an "American Commission on Scientific Nomenclature in Entomology" apparently with the object of proceeding independently. Somewhat later at its annual meeting in April 1942 the American Society of Mammalogists instructed its standing committee on nomenclature "to act pro-tem in the present world crisis for the Committee [sic] on Nomenclature of the International Commission." The Mammalogists' committee felt that any committee restricted to a particular branch of zoology would be ineffective. Therefore, with the approval of the Society's President and principal directors, this committee entered into correspondence with the entomologists proposing that the two committees, without further authorization, jointly sponsor the selection of a small group of representative nomenclaturists to "take over," at least for the time being. Full cooperation between the two committees proved impractical without great loss of time, so the Mammalogists' committee, after receiving the approval of the majority of the entomologists, selected and organized the group as indicated above. The membership of the Mammalogists' committee which carried this out was as follows: A. Cabrera, E. R. Hall, G. S. Miller, Jr., W. H. Osgood, T. S. Palmer, G. G. Simpson, and G. H. Tate.

The "Council" thus formed is frankly experimental and the method of its genesis is unusual, but those responsible for it have felt that any other method, especially in these times when large general meetings are interdicted, would defeat itself in prolonged discussion and fatal delay. Under restrictions which the Council has placed upon itself it is hoped that it may be a wholly representative and cooperative body. A brief set of by-laws has been adopted in which important provisions are to the effect (1) that the active membership shall not exceed fifteen, (2) that additions and replacements shall be made only from candidates nominated by large associations of zoologists, and (3) that no important action can be taken without first obtaining the opinion of at least two nomenclatural committees of national societies and several individuals not members of the Council. A judicial function is thus implied preceding any legislation.

It does not propose to supersede any existing special nomenclatural committees, but on the contrary it is designed to stimulate them to greater interest and more action. Its postwar status is problematical, but, at least as a temporary measure and an effort in a direction urgently needing attention, it is hoped that it may find support. At an early date it is proposed to increase the membership from nine to eleven in order to cover important branches of zoology which are not now well represented.

The by-laws giving details of proposed action will soon be available for distribution to any interested zoologists who may apply for them.—Wilfred H. Osgood, Secretary, *Field Museum of Natural History, Chicago, Illinois.*

OBITUARY NOTICE

LEONHARD STEJNEGER

1851–1943

Dr. Leonhard Stejneger, honorary member of the American Society of Mammalogists, and head curator of biology at the U. S. National Museum for more than 30 years, passed away, after a short illness, on February 28.

Born in Bergen, Norway, October 30, 1851, Dr. Stejneger received his formal training at Frederic's University, Christiania, and came to the United States in 1881. He immediately became associated with the U. S. National Museum and was appointed Assistant Curator of Birds in 1884, continuing in that capacity until 1889 when he became Curator of Reptiles. In 1911, he was elevated to the position of Head Curator of Biology, but his main interest continued in the field of Herpetology.

Dr. Stejneger did much to advance the scientific knowledge of amphibians and reptiles, living as he did in an era of unusual opportunity. Associating with such men as Spencer Fullerton Baird, C. Hart Merriam, Robert Ridgway, Elliot Coues, Edward Drinker Cope, and others of that galaxy of naturalists assembled in or near Washington, D. C. in the last two decades of the nineteenth century, Stejneger doubtless received inspiration and encouragement to carry forward his work in North American natural history. The knowledge of North American birds at that period was considerably advanced, but little progress had been made in Herpetology and Mammalogy. With Merriam and his staff energetically engaged in conducting biological surveys of North America, quantities of new scientific materials poured into the National Museum, providing unsurpassed opportunities for distributional and systematic studies of amphibians, reptiles, birds, and mammals. Stejneger made the best of his opportunities, reported upon the reptiles and amphibians accumulated in many of the earlier surveys, and soon became recognized as an authority in the field.

He accompanied some of the early expeditions of the "Biological Survey" as herpetologist, but his activities were not restricted to Herpetology alone. In 1895, he visited the Commander Islands at the invitation of the U. S. Fish Commission to study fur seals and subsequently he became a member of the Fur Seal Commission, contributing in large measure to the program now in effect to manage the fur seal herds of the North Pacific. He also was an accomplished ornithologist, a Fellow of the American Ornithologists Union, and author of several scientific papers on birds.

In all, his life was full and fruitful and with the passing of Leonhard Stejneger, America lost one of its few all-round naturalists.—W. B. Davis

ity to recognize birds by their notes or by catching a glimpse of them in the field when he was only a boy.

He married, on June 26, 1911, Sarah Moody Cushing, had a daughter Elizabeth Cushing Allen, now Mrs. Arthur Gilman, both of whom survive him.

Allen travelled widely. He knew the mountains, the fields, the dunes, and the meadows of New England as few ever knew them and while he never wrote anything of a popular nature concerning his travels, he often talked of them, relating his experiences in a most whimsical way and with a high degree of humor which was utterly charming, for he drew on a gigantic fund of power to quote from all sorts of literature to adorn his tales.

In 1903, in company with Owen Bryant and myself, he went on a long cruise on a sponging schooner in the northern Bahamas which almost turned out to be something of a disaster, for the islands were visited by an epidemic of the most virulent dengue fever and a prolonged drought. Fresh water was usually caught by tricing up sails during the heavy tropical showers which were normally to be expected almost daily and to these troubles was coupled a cessation of the trade winds, so the vessel lay becalmed and the whole group even tried eating young cormorants, herons, and the like, garnered from rookeries in the coastal mangroves. Allen used to laugh about this as long as he lived. The number of interesting novelties turned up on this voyage was quite unexpected.

In 1906 he went to Labrador with Dr. C. W. Townsend. In 1909 to East Africa with Doctor William Lord Smith and Gorham Brooks; and who can ever forget the tale of his being helped climb a spiny Acacia by the antics of an angry rhinoceros close at his rear. In 1910, with Professor C. T. Brues, he visited the island of Grenada in the West Indies. Here again the booty was exceptionally rich, for Allen was not only a skillful and resourceful trapper but, as is so often the case with small, slight persons, he was absolutely tireless and with an ability to walk and carry a load which was a source of wonder on numberless occasions. In 1912, he went back to Africa with Doctor John C. Phillips. This time, with a caravan, they travelled through the Eastern Sudan along the course of the Dinder River and the Blue Nile. One can hear Allen, now, mimicking the broken English of George, the Greek caravan leader, imploring Phillips to purchase great stores of objects of religious art, in Khartoum, of all places. "Little Christs and small, cheap Virgins; these be very good if Abyssinian poachers raid our camp."

After this journey he remained in Cambridge for many years, caring for the mammal collections in the Museum and writing prolifically until, in 1926, he went with Strong, George Shattuck, Bequaert, and Harold Coolidge to West Africa, where, in Liberia and the Belgian Congo, he collected with his usual skill and industry. Having returned for a few years more of brilliant research and writing, he made an expedition to the Serra de Paranapiacaba in southern Brazil. Doctor Afranio do Amaral, the distinguished Brazilian naturalist, had been working in the Museum and suggested this area as being little known, and was able to provide many facilities in Brazil for which Allen reciprocated by giving some conferences while in Sao Paulo, quite in the Museum tradition, for

Professor Louis Agassiz had done the same thing, bringing Harvard to Brazil in 1865. His last foreign journey was, I suspect, the most enjoyable of them all, for who could have asked for a greater privilege than going to Australia with William Morton Wheeler.

Details concerning the positions that Allen held in the Boston Society of Natural History, the American Ornithologists Union, the American Society of Mammalogists and this University are set forth in the admirable notice of his life prepared by his old friend, Austin H. Clark, which appeared in SCIENCE for March 13, 1942.

Garman remarked many years ago that "Wyman was the Johannes Müller of America." In appearance and in intellectual qualities, Allen was astonishingly like his kinsman, Wyman. Indeed, during the last few years, we have said repeatedly how strikingly Wyman-like Allen was growing. Like Wyman, his lack of interest in selling his wares in the scientific marketplace, his utter unconcern with praise or credit, his singleness of purpose and gentleness and purity of spirit were beyond all praise. Allen never wore his religion on his coat sleeve but was intelligent enough to derive deep satisfaction from being willing to deify a mystery and worship it according to the form prescribed by the Episcopal faith of his fathers.

When something over a year ago there was a celebration held in the Museum to take note of the fact that Allen had published three outstanding books in a single year, I made a few reminiscent remarks and recalled the fact that a line in that surpassingly beautiful hymn, taken from the Liturgy of St. James, might well be considered as a behest which Allen had obeyed all his life, "Ponder nothing earthly minded."

By Barbara Lawrence

It is not easy to write of Dr. Allen. Sitting in his office this dreary January day with the fog so thick that one scarce can see the tower on Memorial Hall, I half expect to hear him say: "You know, I often think I'd like to live in a desert;" and I am reminded of his comment on the sunny, longer days after the turn of the year: "Well, it looks as if we might get through another winter." Indeed, the sense of his kindly presence stays in this place where he worked such long hours studying, questioning, finding out, never losing sight of the fact that it was living creatures he wished to know about, not just dried up remains.

His contributions to the subjects of mammalogy and ornithology have been discussed elsewhere. His research was tremendously important to him and yet he never forgot that he was a Curator as well, and the work of making a rapidly expanding collection available to all who might need to use it was never neglected. Feeling as he did that: "A foolish consistency is the hobgoblin of little minds. . . ," he avoided all elaborate systems and with a minimum of carding and listing kept the collections readily accessible. In his eyes, the material was here not for him alone to study as he saw fit: it was in the museum to increase the sum total of knowledge about mammals. With this in mind, he was

ever ready to help those who wished to use it, whether eminent colleagues or undergraduate students; whether they wished advice and counsel and his wise opinion or whether they merely wanted to look and see. The informality of the department under his aegis was delightful, anyone was free to come no matter for what purpose. How often I have seen him, interrupted at his work, marking the margin of some manuscript and laying it aside to greet some questionning visitor with his friendly: "No you're not disturbing me at all." So the morning would pass, the guest would leave, and he would look at the clock: "What, twelve o'clock already," and when really pressed for time he would add solemnly, "For are there not forty-eight hours in the day?"

For those who worked under him, he was unfailingly considerate, never impatient, never faultfinding, never demanding, and yet time and again I have seen him with his judicious praise and gentle suggestion teach the clumsy-fingered to clean skulls almost as delicately and as well as he himself could. If, in addition, he could interest his assistants in mammals he was more than pleased. Indeed, he was always at great pains to vary the tasks of the newcomers in the department so that they would not find the work tiresome and, instead of turning over to them the more tedious chores, he often did them himself, at the same time encouraging his helpers to start research projects of their own.

Perhaps the time thus spent would have finished his paper on New England mammals and yet one feels sure he felt that the continuity of the naturalist's tradition of scholarly work was far more important than any single project he himself might complete.

By William E. Schevill

Although Dr. Allen, like most museum workers, spent by far the greater part of his time in indoor work, he much preferred the field. He enjoyed studying his animals in the museum collections and the library, but he never lost sight of their living existence in the wild, and most relished his scattered opportunities to study them there. He used to observe ruefully that our actual knowledge of the living animal could in far too many cases be summed up: "When we found it, it ran like hell, whereupon we shot it."

I had the good fortune to be with Dr. Allen in Australia in 1931, when he and I shared several trips in the dry country. I think he liked desert and semi-desert above all other sorts of country. Dr. Allen was then 52 and allegedly in delicate health, but his endurance was greater and much quieter than most youngsters'. His desert camps were as informal as any bushman's—more so than most, for only the blackfellows had less camp gear than Dr. Allen. Provisions were never much on his mind (even when among hotels and restaurants he was an ascetic eater, which was just as well, in view of the many inferior eating houses a back-blocks traveller has to cope with), for all he cared about was to eat just enough to operate on, and never mind the trimmings. When we were on the Houtman Abrolhos, the rains had failed and water was low; he cheerfully and quietly worked for a fortnight on a ration of two cups of water a day, including what was used in cooking.

He was no "sportsman," and often went years without handling a gun, yet he was a competent wing shot. In our first few days on West Wallaby Island we had found the nesting ground of only the more abundant of the two shearwaters so numerous there. These (*Puffinus pacificus*) we collected easily by walking among them and picking them up, but the other species (*P. assimilis*) we then knew only by its call and vaguely glimpsed silhouette as both kinds together flew over on their trips to and from the sea before dawn and after dusk. Accordingly, Dr. Allen waited on the beach at dusk, and as the squalling cloud of birds passed over, he unerringly picked out the uncollected species. He had only the brief moment as they flew across the faint western afterglow, yet he brought down every bird he shot at and made no mistakes. Each one, as I retrieved it with the aid of an electric torch, proved to be *assimilis*,—which a few days later we collected more simply in its burrows. That this was not just his lucky day was clear from Dr. Allen's consistently dependable shotgun work under all conditions. There is a tale, which I did not hear from him, of his shooting bats by firelight in Africa when he had one arm out of commission in a sling.

Dr. Allen was always grateful for any help that came, but did not much seek it, and never let its absence turn him from his work. He did admit that finding himself all alone on a beach with a dead whale made him feel a bit snowed under. I remember him spending hours laboriously scraping the fat from the skins of the mutton birds and the blubbery little wallabies of the Abrolhos. Although he often prepared specimens that others had had the fun of catching, he customarily credited the material to the captor alone.

It is ordinarily expected that companions quarrel and fall out under the routine irritations of camping and cruising, but Dr. Allen did not bear this out. He accepted his disappointments without fuss or petulance, though not with any unnatural polyannishness. Sometimes he took refuge in one of his characteristic pat remarks or quotations. Once when a melancholy acquaintance had subjected him to an exhaustive inventory of his woes, Dr. Allen smiled cheerily at him and said mildly, "Well, we none of us come out of it alive."

His alert and lively interest went far beyond his professional preoccupation with mammals and birds. He was a proper naturalist, and noticed all sorts of living things and their setting in the world. He had the happy quality of sharing this interest with his companions in a serenely pleasant and unpedantic way, with no faintest hint of the dusty lecture room. It is this quiet joy in the field that I remember most clearly of him.

By Sherwood L. Washburn

Many books and articles constitute a lasting memorial to Dr. Allen's intellect and industry. Unfortunately, there is little in these scientific achievements that reflects the genial personality and kindness of their author. Everyone liked Dr. Allen.

Dr. Allen was never too busy to help a student. Every year he used to explain the differences between African and Indian elephants' teeth to student after student, although this was all in the laboratory instructions. Anyone who

came into the mammal department got as much of Dr. Allen's time as he wanted. Sometimes at the close of the day Dr. Allen would remark, "Life is one long interruption."

Students who came for a reference often borrowed Dr. Allen's books and reprints. He cheerfully loaned them year after year, although all too frequently they failed to return.

No student could work about the mammal department for long without being influenced by Dr. Allen's patience and attention to detail. The Peabody Museum used to send over tray after tray of fragments of animal bones. Seeing Dr. Allen sorting and identifying these tiny pieces was a source of inspiration to the student who was having difficulty recognizing whole skulls in the laboratory.

Once while studying galagos, I noticed one that had been shot to pieces. Someone had sewn each little scrap back into place and made an excellent study skin. The collector's tag showed that the man who had gone to all that trouble to save one specimen was G. M. Allen. Later in Borneo when specimens were brought into camp late and in bad condition, when I was tempted to let just one go, I remembered that galago and did my best.

A trip to the mammal department was always an adventure for the student. One never knew what to expect. Dr. Allen might be doing anything from drawing a tiny bat's skull to macerating whale bones. He might be reminiscing about Africa or telling a man with a particularly foul bit of sewage sludge, "I am afraid that is not ambergris."

When classifications change, when new data supplant that which were available to Dr. Allen, his students will still think of his kindliness, industry, and patience. Perhaps, we can pass on to our students some of his interest and devotion to study. Perhaps, his greatest contributions aren't published but live on in the lives of his friends and students.

By Mary B. Cobb

Although Dr. Allen resigned as Librarian of the Boston Society of Natural History in 1928, he never lost his keen interest in the Library nor his concern for its problems. In all our endeavors we could rely on that sympathy as much as on his great fund of knowledge.

His memory was phenomenal. "Dr. Allen, do you know whether anything has been published on this subject?" "Oh, yes, didn't B—— write a good paper in the Zoological Society's *Proceedings* about 1898? I'll find it for you." It was hard not to impose on such generosity. But there was never a hint that he felt it an imposition. The manner of conveying information, too, was a pleasure to see. Never a suggestion that you ought to know, nor yet that of course you *wouldn't* know. Instead he implied somehow that you knew, but that it had slipped your mind for the moment. "Why, that's one of the (such-and-such animals),—isn't it?"

Praise was apt to embarrass him. The nearest I ever saw him come to out-

spoken annoyance was when I read gleefully what Casey Wood said of his work on Pleske's "Birds of the Eurasian Tundra." ". . . translated and edited by Dr. Glover M. Allen, although, with characteristic modesty, he suppresses any mention of that fact in the text."

When he came over to our Museum from Cambridge there were always queries, as soon as his presence was known. Curator, Preparator, Director, visitors, as well as Librarians, would need him for something that no one else knew about. But he never held court. When the questions were answered he would slip away, and be found in a far corner of the stack, consulting the Bombay Journal, or refreshing his memory on what Gesner had said of a certain mammal.

Looking back it seems almost humorous that the self-effacement of a lifetime should have failed to achieve its purpose; that a total lack of aggressiveness could have proved so dynamic. As Sir D'Arcy Thompson has said of another, he had "that singular and indescribable quality of *character*, which is never to be mistaken, never to be concealed, never to be sufficiently valued and admired."

One of the amazing things about Dr. Allen was the amount of work he accomplished, and this without any dashing about or electrifying the atmosphere around him. His motto might have been, "*Ohne Hast, ohne Rast*". There were no waste motions; one noticed this even in the rapid but clear writing with which he took down a reference. He sighed sometimes over his tendency to set himself enormous tasks, and hardly expected that he would live to see them accomplished. Many of them he did, happily for him and for science. His earnest wish, often expressed, that he might "do something for Africa" found fulfillment in the great checklist of African mammals; and his "Bats" have made many friends for one of his favorite creatures. In odd moments he made a complete Index to the first fifteen volumes of this Society's *Proceedings*, a sheer feat of industry.

Others will have told of his wide range of interests. It was my delight to add to his collection of animals in ancient art. Whether they were Persian, Chinese, Aztec or Egyptian, crude, conventionalized or fanciful, he could always tell what creature was represented, and how important it was to that particular civilization. The Chinese art, with its frequent use of bats, had a special interest for him. He would sketch rapidly the Five Bats of Happiness in a circle, and in a whimsical moment use this for his "mark" on a card; though more often a little bat would follow his signature.

It was pleasant to see the touches of humor that relieved his habitual gravity. With what relish he would quote Topsell's description of the "Su"—". . . and when she seeth the hunters come about her, she roareth, cryeth, howleth, brayeth, and uttereth such a fearfull, noysome, and terrible clamor, that the men which watch to kill her, are not thereby a little amazed . . . And this is all that I finde recorded of this most strange beast." A line from the "Bab Ballads" or from one of Kipling's poems would fit some other occasion or person; but his humor was always kindly.

When Jeffries Wyman died in 1874, James Russell Lowell wrote a sonnet to

him, which is remarkably appropriate to Wyman's younger cousin, Glover Allen.

"The wisest man could ask no more of Fate
Than to be simple, modest, manly, true,
Safe from the Many, honored by the Few.
. . . . . .
To widen knowledge and escape the praise,
Wisely to teach, because more wise to learn,
To toil for Science, not to draw men's gaze,
But for her lore of self-denial stern;
That such a man could spring from our decays
Fans the soul's noblest faith until it burn."

RELATIONSHIPS OF THE ORDERS OF MAMMALS

By William Diller Matthew

(Edited and Annotated by George Gaylord Simpson)

[It is doubtful whether any student ever achieved a more comprehensive and balanced knowledge of all the Mammalia, living and extinct, than the late W. D. Matthew. His ideas of the relationships of mammals are therefore worthy of attention and study, even after a lapse of years. He published broad discussions of mammalian affinities within particular orders, such as the Artiodactyla, or at particular times, such as the Paleocene, but he did not publish any concise, general statement of opinion as to the relationships of all orders throughout mammalian history. An unsigned and undated manuscript giving such a statement has recently been found. It is certainly by W. D. Matthew and internal evidence dates it as probably 1925 and surely within a year of that date. The manuscript consists of a sketched phylogenetic chart and of 27 notes corresponding with numbers on the sketch. The chart has been redrawn, without any emendation, and it is here presented along with Matthew's comments on it. Editorial notes are added in brackets, like this introduction, where there is reason to believe that Matthew modified his opinions before his death in 1930 or where subsequent discoveries have made a decisive change in the evidence. This is done in order not to mislead students in publishing a paper written about 17 years ago, but the editorial annotation is not critical and does not alter the fact that Matthew's brief manuscript is valuable today and not only historically. All statements not in brackets are as Matthew wrote them.]

1. *Tritylodon* is the only representative of the Multituberculata in the Lower Jurassic. It belongs to a quite distinct family from the Plagiaulacids and is not ancestral to them. The earlier history of the order is unknown. Earlier views on its affinities may be disregarded as they were based on a very small fraction of the anatomical data now available. Among recent authorities, Broom, whose acquaintance with *Tritylodon* is especially intimate, regards the

order as nearest to Monotremes. Gidley, from a study of skull and part skeleton of *Ptilodus* concluded that it was a Diprotodont Marsupial. Gregory regards the order as related to the Marsupials but distinct enough to be of ordinal rank. Matthew and Granger, with additional skeleton parts of *Ptilodus*, concluded that although closely parallel to Marsupials it was as distinct from them

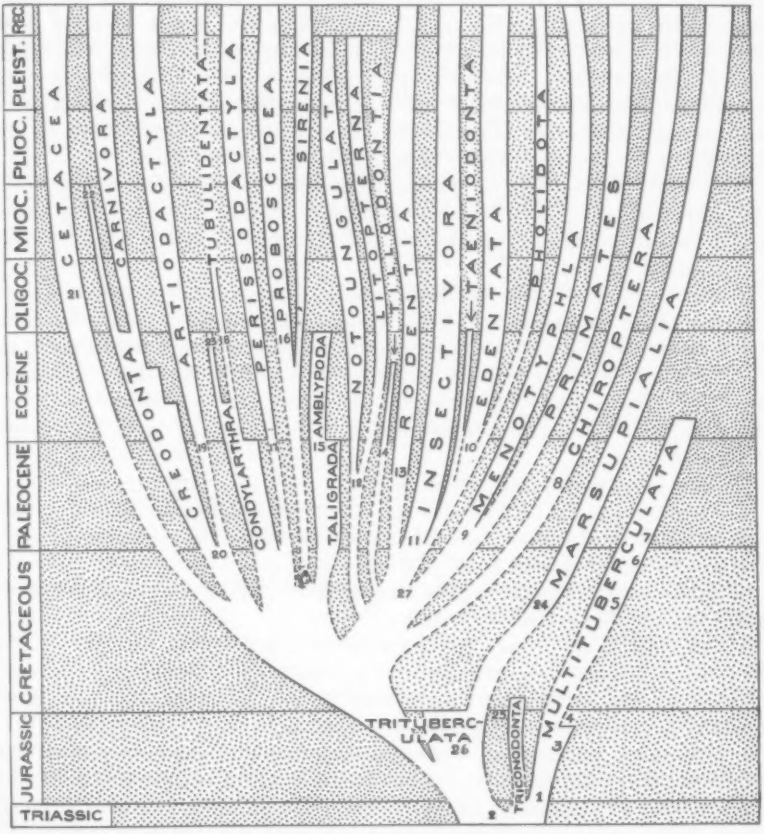

FIG. 1.—Phylogeny of the orders of mammals according to W. D. Matthew's views of about 1925. Numbers on the chart refer to comments in the accompanying text.

as they are from placentals and should stand in a fourth subclass Allotheria separate from the Metatheria and Placentalia (Eutheria of Huxley), all three belonging in a group together (the Eutheria of Gill), however, as against the Prototheria (order Monotremata).

[Granger and Simpson later maintained that the Allotheria should be distinguished from all other mammals, not placed with the marsupials and placen-

tals in a group contrasting with the Prototheria. Matthew accepted this modification. He also later referred *Tritylodon* to the late Triassic, as do most students, rather than the early Jurassic.]

2. The Triassic mammals are so imperfectly known that it is scarcely worth while to attempt any more definite suggestion as to their affinities. *Microlestes* is known from a few teeth which have some suggestion of affinity to the Multituberculates but may have no near relationship. *Karoomys* is based on a lower jaw fragment without teeth of which the best one can say is that it may be a Multituberculate. *Dromatherium* is based on a nearly complete jaw but it is an open question whether it (with *Microconodon*) belongs to a mammal or to a mammal-like reptile (Theriodont), in view of recent researches upon this latter group by Broom, Watson, Gregory, Haughton and others.

[This discussion of Triassic mammals excludes *Tritylodon*, see above, and omits *Tritylodon*-like teeth from the European Triassic. Simpson later maintained that *Karoomys*, *Dromatherium*, and *Microconodon* are reptiles and this was accepted by Matthew.]

3. The Stonesfield slates (Middle Jurassic) contain three diverse types of fossil mammals. *Amphitherium* has a typical tritubercular dentition, *Phascolotherium* with phocoid teeth and *Stereognathus*, an upper jaw with teeth suggesting *Tritylodon*. The last is possibly referable to the Tritylodontidae. *Phascolotherium* perhaps to the Triconodonts, and *Amphitherium* may be a proto-placental; but all these affinities are speculative. No evidence of Plagiaulacids at this horizon.

[On the so-called trituberculates see 26.]

4. The Purbeck and Morrison mammals include *Plagiaulax*, *Triconodon* and a group of "trituberculates" related to *Amphitherium*. The last may include both proto-marsupials and proto-placentals.

[Matthew later accepted Simpson's separation of a fourth order of mammals in the Jurassic, the Symmetrodonta.]

5. The Belly River Upper Cretaceous includes Plagiaulacids and Cimolestids, the latter unmistakable marsupials rather close to the opossums.

[Matthew later placed the "Cimolestids" in the Didelphidae and abandoned the dubious name Cimolestidae.]

6. The Lance fauna (latest Cretaceous) contains the same elements as the Belly River, but a larger variety of genera in each of the two groups, due to the greater number of specimens known. Placentals are doubtfully present in the Lance, certainly in the Paskapoo, unknown in any older Cretaceous faunas but it is probable that the known Cretaceous faunas represent only such mammals as lived along with the dinosaurs in the great coastal swamps. The Cretaceous pro-placentals may have been a dry land or upland fauna.

[Reference of the Paskapoo to the Cretaceous was an error almost immediately abandoned. Unquestionable placentals are now known from the Cretaceous of Mongolia.]

7. The Puerco fauna consists of Plagiaulacids, Didelphids, a number of ? Insectivora, a variety of Taligrada, Condylarthra, and Creodonta, the last three

groups including the bulk of the fauna and apparently rather nearly related. The primary division in the Paleocene placentals appears to be into a Creodont-Condylarth group and an Insectivore group, the Taligrada being related more nearly to the former. These groups continue through the Torrejon, doubtful Primates (Tarsiids?) in the Tiffany-Fort Union-Cernaysian, well specialized bats in the Tiffany. The last of the Multituberculates is found in the Wasatch Lower Eocene.

[Matthew later recognized that the Plesiadapidae were probably true primates, a conclusion made fairly certain by later study. It has also been definitely established that primates occur in the Torrejon equivalent, middle Paleocene, of the Fort Union Group.]

8. The relatively modernized type of Chiroptera found in the Paleocene indicates that they must have branched off from the main Placental stock far back in the Cretaceous at least, but there is no more definite evidence. Their apparent anatomical relationship to the Insectivora suggests remote derivation from a proto-Insectivore stock.

[Citation of Paleocene bats refers to *Zanycteris*, the affinities of which are not quite certain. Unquestionable specialized bats do occur in the Eocene.]

9. The earliest Menotyphla and Primates in the Lower Eocene and Paleocene appear to be quite nearly related so that the affinities of the different genera are variously estimated by different authorities. Derivation from a common stock in the uppermost Cretaceous seems to be indicated. All Eocene Primates are in the Lemuroid stage of evolution.

[As is clear in his other writings, Matthew included *Tarsius* in the "Lemuroid stage" structurally, but not necessarily in the Lemuroidea.]

10. The Lower Eocene Edentates (Palaeanodonts) and the Paleocene Taeniodonts are very primitive and nearly related to the proto-Insectivores of the Paleocene. The Palaeanodonts are not far from being ancestral to both the Xenarthra and Pholidota. The specialized groups of the Xenarthra are not really adequately known until the Miocene (Santa Cruz) in South America. The very fragmentary and doubtful remains recorded from the Oligocene and Eocene (Pyrotherium and Notostylops faunas) of South America may have been much less specialized. The status of the supposed Pholidota of the Phosphorites and later Tertiary of Europe is very doubtful.

[Since Matthew's death unquestionable and fairly specialized armadillos have been described from the Patagonian Eocene. Nevertheless, they tend to confirm his derivation of the Xenarthra from the Palaeanodonta. Later study leaves the relationships of the Pholidota with these groups somewhat more questionable.]

11. The Paleocene and Eocene Insectivora are primitive types with but little to distinguish them from related orders. Specialized Insectivora clearly related to the modern families appear in the Oligocene and the modernization progresses through Miocene and Pliocene. The Leptictidae are the best known of the Paleocene and Eocene types. *Onychodectes* of the Lower Paleocene, although regarded as an ancestral Taeniodont is quite near to these proto-

Insectivora (*cf.* skull and skeleton with those of *Diacodon* of the Middle Paleocene) and not far removed from the Paleocene Creodonts, Condylarths and Taligrades.

12. *Palaeostylops* of the Paleocene of Mongolia and *Arctostylops* of the Lower Eocene of Wyoming are undoubted Notoungulates and more primitive than any South America genera, but already well differentiated in teeth. The affinities of the group appear to be rather with the proto-Insectivora than with the proto-Condylarthra, but pro-Taligrade relations are not to be excluded. In any event the differentiation of the group must date well back in the Cretaceous. The Litopterna are undoubtedly derived from a common stock with the remaining Notoungulate groups.

[Some early South American genera known to Matthew only by incomplete descriptions now appear to be at least as primitive as *Palaeostylops* and *Arctostylops*. I find in Matthew's works no other statement of the unusual view that notoungulates might be nearer the proto-Insectivora than the proto-Condylarthra. Elsewhere he seems to imply acceptance of more or less distant condylarth affinities.]

13. The record of the Rodentia begins with the Lower Eocene at which time the ordinal characters are fully differentiated. Its derivation from proto-Insectivora of the later Cretaceous appears probable.

[A lagomorph has since been recognized in the Mongolian late Paleocene and a true rodent in the American late Paleocene. These probably would not have altered Matthew's opinions, unless possibly to make him place the origin of rodents at an earlier date.]

14. The Tillodonts are not ancestral to Rodents, but also derived apparently from Cretaceous proto-Insectivores.

15. The Taligrada (including Periptychidae) are a primitive group that may stand broadly ancestral to some of the later sub-Ungulate orders, almost certainly to the Amblypoda, perhaps to Hyracoids, Arsinoitheres, Pyrotheres, possibly to Proboscidea; but in no case can the ancestral lines be traced closely enough to assure the relationship. Gregory considers that the Proboscidea point back rather to Condylarth ancestry. In any event there is no very deep-seated diversity between Paleocene Condylarths and Taligrades.

[In support of Matthew's last sentence in this passage, Simpson has since proposed placing the "taligrade" periptychids in the Condylarthra. Later discoveries and studies, *e.g.* by Patterson, make it highly improbable that the periptychids were the ancestors of any so-called amblypods, but support the relationships of the "taligrade" pantolambdids and the "amblypod" coryphodonts. The uintatheres, however, appear to be quite distinct from any of these. Extensive work just getting under way when Matthew died would almost surely have led to considerable modification of his formal arrangement of these groups, although it does not radically contradict his basic ideas as to their evolution.]

16. Proboscidea can be traced back to the Upper and Sirenia to the Middle Eocene, undoubtedly approaching at this stage towards a common stock—as shown in the disputes over the affinities of *Moeritherium*.

17. Perissodactyla are clearly distinct at the base of the Eocene where they first appear in the record, but they approach the Condylarthra so nearly as to point unmistakably to common Cretaceous ancestry.

18. *Orycteropus* appears to be a highly specialized survivor of the Condylarthra, and to have no affinities to the Edentate orders. The order is doubtfully recorded from the Phosphorites of France. *Orycteropus gaudryi* of the Upper Miocene is nearly related to the modern Aardvark, although it deserves generic separation.

[Jepsen has since described a supposed ally of *Orycteropus* from the early Eocene and has opposed condylarth affinities, but Colbert and others reject Jepsen's conclusions and reaffirm Matthew's views.]

19. Artiodactyla make their first appearance at the base of the Eocene, and are regarded by Gregory and myself as having closer affinities to primitive Creodonts than to primitive Condylarths, the Creodont family Mesonychidae and the Artiodactyl family Entelodontidae being in some respects intermediate.

[Matthew continued to support this view of artiodactyl-creodont affinities and nothing has been found to disprove it, but later students incline more toward derivation of artiodactyls from condylarth-like ancestors.]

20. The Creodonta comprise a number of specializations from a common primitive stock, from one of which, the Miacidae, the later Tertiary and modern Carnivora are descended. This includes the Pinnipedes as well as the terrestrial families.

21. The Cetacea are an extremely specialized group at present, but a good deal of this specialization disappears as they are traced back into the Eocene. They may have diverged from the primitive placentals as far back as the middle Cretaceous but probably not earlier. Whether their special affinities lie with the Creodonts as the diagram would indicate, is not clear. The view advocated by some writers that they are derived from the Hyaenodontidae, is quite untenable.

[The origin of the Cetacea is hardly clearer than when Matthew wrote, but studies by Kellogg and others suggest that they may have arisen even before the insectivore-creodont dichotomy and that exclusive creodont relationships are unlikely.]

22. Survival of Hyaenodonts in Oriental and Ethiopian regions (*Dissopsalis*, Lower Siwalik, India; *Metapterodon* from supposed Lower Miocene, S.-W. Africa).

23. The Hyopsodontidae survive until the Upper Eocene although the remaining Condylarths disappear much earlier.

24. The earliest definitive Marsupials are the Cimolestids of the Belly River and Lance Cretaceous. Some of the Jurassic Trituberculates may prove to be Marsupials or proto-marsupials, but too little is known of them to assess their real position. Didelphid marsupials occur throughout the Paleocene, Eocene and Oligocene of North America, the Guaranitic ? Upper Cretaceous and later horizons of South America. The affinities of the Caenolestidae of the South American Tertiaries are between polyprotodonts and diprotodonts, but the

earliest unquestionable diprotodont is *Wynyardia* of the Australian ? Miocene, related to *Phalanger*. This is the only record of the Tertiary land mammals of Australia.

[For "Cimolestids" Matthew would later have written "Dipelphids." It has since been shown that the supposed discovery of a didelphid in the Cretaceous of South America was probably an error.]

25. The Triconodonta are of doubtful relationship. They have been assigned to the Marsupials on quite unconvincing evidence. Simpson considers them as an independent group. Matthew regards the teeth as suggestive of some relationship to the Multituberculata but not close.

26. The Trituberculata may represent the common stock ancestral to both marsupials and placental mammals but the described forms from the middle and upper Jurassic are known only from a few jaws and fragments. The teeth are tritubercular or zalambdodont, the latter type in Matthew's opinion probably a secondary specialization as it is found only in the Upper Jurassic. The number of molars varies, sometimes higher than in either Marsupials or placentals; but that may also be a secondary specialization. Certain genera show a distinct angle of Placental type, but are not otherwise nearer the placentals. Others resemble marsupials in the angle. It is probable that the distinctive characters of marsupials and placentals were at this period in unstable condition, liable to occur in various combinations in the different genera, and not yet of any great taxonomic weight. This is the usual history in the evolutionary record of any group. Synthetic types are common at or near the beginning of the divergence of the different groups not directly ancestral to either of two subsequently distinct groups but combining variously the characters subsequently sorted out into the two groups, with other characters some primitive others aberrant, that have survived in neither. So far as the scanty evidence goes it conforms to this *a priori* expectation in the Jurassic trituberculate mammals. Skulls of these animals recently found in the Cretaceous of Mongolia may throw a great light on the problem.

[Matthew later approved Simpson's revival of the more noncommittal name Pantotheria for the Jurassic "trituberculates." The views as to their affinities here expressed by Matthew antedate similar views supported in some detail by Simpson. The last sentence of this passage suggests confusion of the Cretaceous with the Jurassic "trituberculates," but this was unintentional: Matthew of course recognized that the Cretaceous forms were definitely placentals and that the Jurassic pantotheres were not. Unfortunately the Cretaceous discoveries have not, as yet, thrown much of the hoped light on the problem.]

27. The divergence between Menotyphla and Insectivora is here carried back to the Cretaceous. There is however a somewhat different viewpoint possible. We may regard the Tupaiidae as representing the primary stock from which the Macroscelididae, the Erinaceidae, Leptictidae and Soricoidea are specialized offshoots, while the Zalambdodonts are a parallel but distinct stock. This would bring the Lipotyphlan Insectivores into a corresponding relation with the Primates to the unchanged Menotyphlan stock, and could be represented on

the diagram by shifting the Taeniodont-Edentate-Pholidote sequence to the other side of the Insectivora and closing up the gap between Insectivora and Menotyphla and Primates. Recently discovered Oligocene Menotyphla Erinaceoids and Soricoids lend some support to this hypothesis of relationships which would place *Tupaia* in a position among placentals partly corresponding to that occupied by *Didelphys* among Marsupials, that is, as being an unchanged persistent arboreal type from which various terrestrial and fossorial specializations are structurally derivable.

[The points here discussed vexed Matthew during much of his life and he seems never to have been fully satisfied concerning them. Either of the alternatives suggested by Matthew must be considered possible, but later research inclines to follow Matthew's diagram more nearly than the alternative of his text, at least to the extent of considering tupaioids as nearer to the primates than to the typical modernized insectivores.]

American Museum of Natural History, New York, N. Y.

THE PINE SQUIRREL IN COLORADO

By Robert T. Hatt

In all respects except color the chickaree of the Front Range of the Rocky Mountains of Colorado is a typical red squirrel. My purpose in the study reported in this paper was to determine the extent of the differences between the life history of this mountain species and that of its eastern counterpart. I have published elsewhere (1929) a report on the life history of the red squirrel.

Field studies, covering the periods from June 17 to 21 and July 1 to 22, 1939, were made chiefly in Boulder County, Colorado, from lower to upper timber lines, a vertical range of almost a mile. Headquarters were established at Science Lodge of the University of Colorado, on the lower slope of Mount Niwot, at an elevation of 9500 feet, and about three miles by air southwest of Ward. Many trails and good roads gave easy access to a wide range of ecological conditions.

Observations extended geographically from the central section of Rocky Mountain National Park to Devil's Head Peak, west of Sedalia, and from the lower foothills of the eastern slope to the upper forest of the western. The major forest communities examined were spruce and fir, lodgepole, ponderosa, and limber pine. Burns in lodgepole were studied while the trees were still in flame and at stages of one year, several years, and many years.

The study was made during a period of extreme drought. Indeed, the Longmont (Boulder County) weather station recorded less precipitation in the first seven months of the year 1939 than in any similar period since its records began in 1888, and the Front Range presented the worst fire hazard in the United States during the summer of the study. No drenching rains fell during the time of the study, a condition that no doubt limited the variety of foods available

to the squirrels. As an example, though mushrooms are said to be common in this area in wet years, no fresh specimens were seen at this time.

I am indebted to the officers of the University of Colorado for their kindness in allowing me to use the facilities of Science Lodge, and particularly to Mr. Hugo Rodeck, Director of the University of Colorado Museum, who was a gracious host and adviser. The study was conducted under the auspices of the Cranbrook Institute of Science.

POSITION AMONG THE SQUIRRELS

The pine squirrel (other names: spruce squirrel; Fremont's chickaree) studied is *Tamiasciurus fremonti fremonti* (Audubon and Bachman), the type locality of which is the "Rocky Mountains", probably the park region of central Colorado. Nominally a species with four subspecies, that extend through the Rocky Mountains from about the northern Colorado border to many of the isolated ranges of New Mexico and Arizona, it differs from the red squirrel, *Tamiasciurus hudsonicus* (Erxleben), in having gray bases to the hairs of the ventral surface. It is but the southern Rockies' representative of this species, and differs in its habits no more than do red squirrels of one subspecies living under different environments. (See Hatt, 1929, p. 43.)

Like the other members of the genus *Tamiasciurus* (tree squirrels that lack a baculum) it is associated strongly with the conifer forests of the cooler zones and finds its principal food resources in the seeds of these trees. As do the others, it also nests principally in the trees, leaps agilely among the crowns when a highway of branches is not available; jumps from great heights to escape on the ground when retreat is otherwise blocked; stores quantities of cones underground in large caches or singly; harvests fungi, dries and stores them in the tree branches; is partially carnivorous; vociferously and variously scolds the invader of its domain; leaves conspicuous middens at its favorite feeding sites; tunnels extensively in the soil and snow when conditions are favorable. Although for over a century the squirrels of this group have been considered the most terrestrial of North American tree squirrels, owing to their construction of tunnels, their frequent descent to the ground for escape, their occasional nesting under the earth or in such earthbound sites as stone fences, it must be observed that Grinnell and Storer (1924, p. 204) considered the California representative of the group (*T. d. douglassi*) a particularly arboreal squirrel.

In common with North American tree squirrels of the genus *Sciurus* it undergoes no aestivation or hibernation, although ordinarily remaining in the shelter of its nest in periods of severe cold or storm. Like these other species it constructs bulky nests, feeds and seeks immediate safety, principally, in the trees. It may, like other tree squirrels, forage on the ground and store food in pockets made in the ground.

THE PELAGE

The pelage characters of the red squirrels have been described in my 1929 monograph. Notes here relate to that description.

PLATE 1

UPPER: Forest of lodgepole pines. Such forests in their great extent support a large but not a dense pine squirrel population. Science Lodge, Boulder Co., Colo., June 19, 1939.

LOWER: Mature forest of spruce and fir. Pine squirrels are common in this and similar forests but not easily studied because of the height of the trees and the abundance of undergrowth. Near Cache la Poudre lakes, Rock Mountain National Park, July 2, 1939.

PLATE 2

UPPER: Timberline trees. Pine squirrels occur in the dense forests a short distance below timberline but no sign of them is observed in the stunted trees here or just above. Mount Baldy, Boulder Co., Colo., June 18, 1939.

LOWER: In yellow pine forests such as this the pine squirrel is not found, probably because of the lack of tree-highways, the lack of good nest shelter and the difficulty of feeding on the robust cones of the yellow pine. Near Nederland, Colo., 9000 feet, June 19, 1939.

Sexual differences in pelage are not extensive. The male has more hair on its ears and has the nasal stripe darker than that of the female.

The broad black band of the lateral tail hairs is so well developed at the tip of the tail that it produces in effect a black end, probably analogous to the prominently marked tail tips of such long-tailed animals as the kangaroo rats—a pattern tending to protection through distracting the attention of a potential predator to a non-vital part of the anatomy.

The squirrels in winter, besides increasing the warmth of their coats, lose the dark lateral line. The significance of such a change, if there is significance to it,

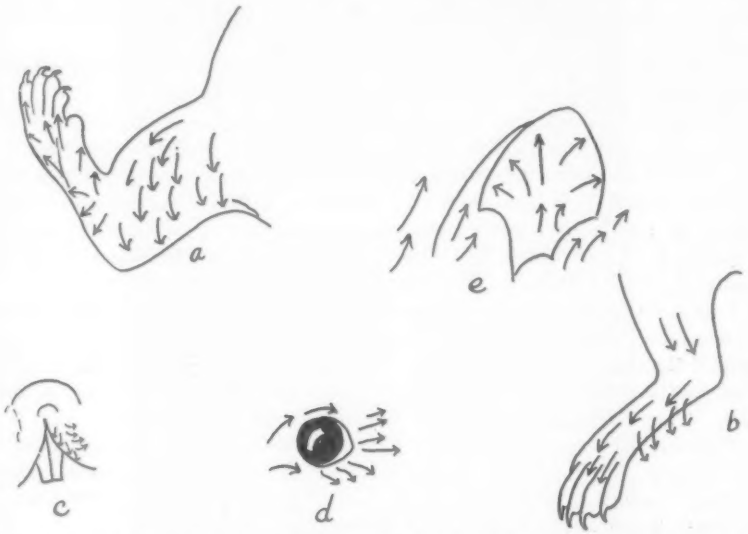

FIG. 1. Details of hair growth patterns in the pine squirrel. *a*. left forearm, outer surface; *b*. left hind foot, dorsal surface; *c*. lips; *d*. left eye region; *e*. left ear.

is obscure. A squirrel of any pattern would be prominent on the snow and the evergreen trees among which the animals live the year around do not change conspicuously with the seasons. The longer ear tufts of winter may persist into the early summer, for at 10,500 feet, on June 18, I observed a female on which they were conspicuous.

The tactile hairs are as I have described them in the red squirrel, except that in the few pine squirrels collected the carpal vibrissae were seven instead of three, the submental group occurred in a tuft of about a dozen small white vibrissae, and there was also a small group of short tactile hairs over the scapulae.

Details of the direction of hair growth as drawn from an adult male pine squirrel, and not shown in my red squirrel drawings are shown here (fig. 1).

INDICATIONS OF ITS PRESENCE

Squirrels at times are secretive and it is possible to pass through a forest in which they are abundant without seeing the animals, yet by their signs their presence is easily known. The specialization of the pine squirrel's food habits invariably results in the accumulation of piles of debris, which, where occupation of the site is long continued, become virtual monuments to their makers. Searching for squirrels one soon learns to judge their abundance by the amount of food litter. Where an area is newly occupied or but occasionally visited in a distant foray, cone litter is light and scattered, but not infrequently seen on stumps, logs or below isolated barren tree branches which served as feeding stations. Since no other animal in the range of this squirrel produces such debris, there need never be doubt as to the identity of the sign.

Freshly harvested cones, lying on the ground, with or without attached branchlets, are also good evidence of the presence of the squirrels.

Pine squirrel nests serve as proof of the occurrence of the squirrel, except that their age is not always apparent since a nest may stay fresh looking for more than two seasons, and from the ground an old nest is not always recognizable as such. In thick growth it is also possible to mistake a bunch of mistletoe or witches broom for a nest, particularly inasmuch as the squirrels do on occasion use such a growth for a nest foundation. Nests are poor criteria too because of the difficulty of locating them in thick growth.

Tree stored mushrooms may serve to indicate the presence of pine squirrels. I have found this true with the red squirrel (Hatt, *op. cit.*, p. 118). Had I studied the pine squirrel other than in a year of exceptional drought in which there was no mushroom crop, I probably would have found such stores in Colorado. They have been reported in other seasons by Mr. Rodeck.

The least useful indicator of squirrel presence is the feces. These are observed occasionally on middens or logs, but they seem to be dropped promiscuously, except in the nest. When fresh, they are ovoid to oval, about two millimeters in diameter, thrice this long and brownish black.

THE EXPRESSIVE CHICKAREE

The pine squirrel has all the vocal tricks of the red, and like the red, drums with its hind feet when nervous. Capable of scolding a visitor as long as the visitor will stay, the squirrels are, nevertheless, very wary on occasion and even in the center of a large colony complete silence often reigns. July 14, I visited a dozen great middens and at some stopped from a quarter to a full hour but at none did a squirrel make its presence known. To what extent the voice is the "no trespass" indicator of a squirrel's territory, is a matter for further study. Gordon (1936, p. 171) has well compared the use of the voice to that of birds marking out their territory, but the squirrel uses its voice in too many ways for a single usage to be assigned all vocal effort.

A squirrel on one occasion started scolding me from a distance of 100 yards, when I was in clear sight. Another time a long-crested jay became excited at my proximity. A pine squirrel at least 200 yards away and certainly unable to

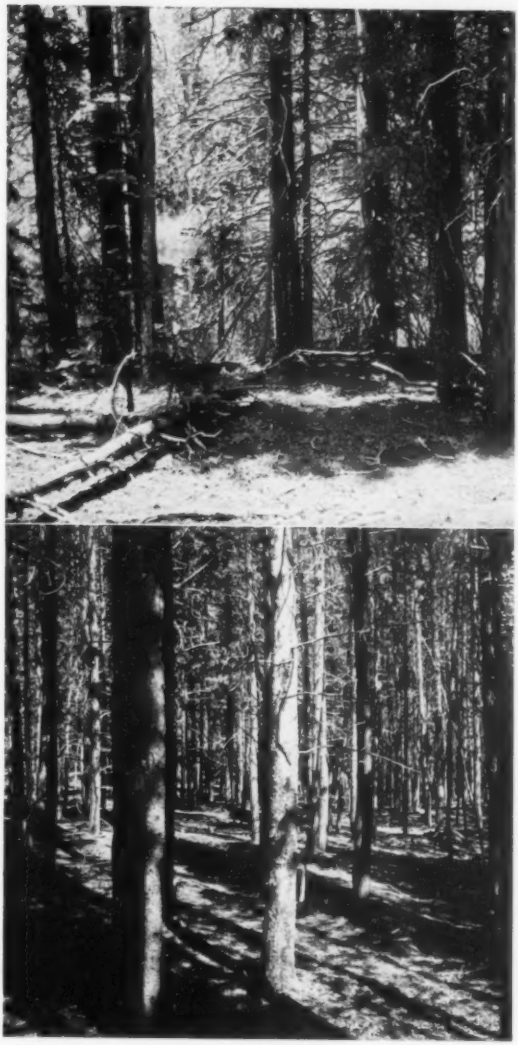

PLATE 3

UPPER: A dense stand of spruce and fir by a morainal lake. Pine squirrel midden is heavy and a nest may be seen at the top center. Above Science Lodge, July 14, 1939.

LOWER: Dense stand of lodgepole in which five pine squirrels were found in ten acres. The highlighted tree in the center is a dead lodgepole from which much bark has been removed by the squirrels. Near Rollinsville, Colo., July 18, 1939.

PLATE 4

UPPER: Pine squirrel midden on a stump. Science Lodge, June 20, 1939.

LOWER: A deer mandible, largely gnawed away by pine squirrels, lying on a midden. Science Lodge, July 11, 1939.

see me took up the scolding and continued it for twenty minutes without interruption or major change of location.

A male and female on opposite sides of a large midden area (July 5) scolded one another for several minutes When the male came to the female's side of the midden, she chased him 150 feet through the trees and over the ground. Long (1940, p. 175) observes that the squirrels are "quiet and subdued" during the breeding season.

The voice has occasionally a peculiar double quality, combining alternate piping and chucking.

METHODS OF LOCOMOTION

The pine squirrel travels in the zone of the trees, through their tops, among their roots. It moves about in the same manner as the red squirrel, whose locomotion I already have described. The largest leap that I observed for the pine squirrel was three feet from the top of a stump to the trunk of a standing fir. The squirrel landed head up, at a point on the same level from which it took off. This is an ordinary accomplishment for a tree squirrel.

The pine squirrel on the ground, (as is true of the red) when frightened by a person near it, will ascend a tree to get away from danger; then, if sufficiently provoked, make away through the trees for perhaps a hundred yards, but, commonly, then descends to the ground to move farther away.

If one climbs after a squirrel, it will leave the tree either by crossing to other trees whose branches are near, or, if isolated, it may jump. One one occasion I saw a leap of 25 feet to the ground. The squirrel appeared unharmed after landing and immediately escaped to other regions. Once a squirrel, instead of leaping when cornered, ran directly past me on the trunk to reach the ground.

Squirrels hunted in winter, I am informed by Mr. Rodeck, first resort to the trees, but, when at a sufficient distance, they descend to the ground and enter tunnels.

The red squirrels, as has been commonly observed (Hatt, *op. cit.*, pp. 33, 68–74), characteristically construct extensive tunnels in snow, earth, and rotted logs, in which they may build nests or store food. It is reported to me that snow tunnels of the pine squirrel are common in winter in Boulder County, as would of necessity be true with food resources largely stored below ground. Although extensive snow banks remained in the forests where squirrels were common in the summer of 1939, I never found a trace of a squirrel tunnel in them. Certainly there was no necessity for a squirrel to enter the summer snow banks, and any pleasure that might be derived from snow tunnelling was supplanted by the other pleasures of summer.

The construction of storage pockets in soil and in squirrel middens, was commonplace, as I note elsewhere in this report, but nowhere did I find long tunnels such as those characteristic of the eastern red squirrel. This would appear to be in consequence of the shallowness of soil and its coarseness in the habitats occupied by the pine squirrel. Such hardy diggers as pocket gophers (*Thomomys*), golden-mantled ground squirrels (*Citellus lateralis*) and chipmunks (*Euta-*

mias) occupying the same or adjacent habitats, do successfully move the earth, but the pine squirrel is physically less well equipped to work soil the character of slightly decomposed granite. The ground in stands of yellow pine and limber pine is usually very coarse and rocky and may be the prime deterrent factor, or a contributory factor to the limitation of pine squirrel occurrences in these stands. Sufficient workable soil for cone storage may be important.

Such tunnels as were observed in the course of the field study were with few exceptions short, under logs or in middens, and barren of any foreign material other than a few cone cores. Exceptions were found in a stand of small spruce, fir, and lodgepole on the bank of Rainbow Creek, near the end of Maxwell Road. Here the unusual condition of deep soft forested soil provided the examples that proved the rule that the squirrels burrow where favorable forest and favorable soil occur together. Extensive matting of large roots interfered with extensive following of tunnels at this site.

One of the short burrows in the stand was followed to its end. It started in a midden and extended with a single fork to a depth of ten inches at two and one-half feet from the entrance. In the end of the shorter fork, at a depth of eight inches, were stored one lodgepole cone and one spruce cone. Near the tunnel, but unconnected with it, was a pocket ten inches deep containing eighteen spruce cones in the moist cold soil.

Tunnels in middens were found extending to a depth of twelve inches, but none was so deep in the soil.

In an area of lodgepole near Rollinsville, in which particular note was given to distribution of squirrels, nests and middens, careful search was made for an underground nest in an area 50 feet in diameter, much occupied by a squirrel that was not known to be associated with a tree nest. Every ground-opening in this area was carefully followed out, but most were but shallow pits and none was over 18 inches long except for one, following below a log, that ran for 36 inches.

THE DAY'S CYCLE

In late June, the mountain nights were bitter cold and at no time was the day hot, but in July, accentuated by the dryness of the year, nights were comfortable, days almost hot, to my way of thinking.

The squirrel schedule did not seem to be influenced by the observed temperature changes from June to July. At daybreak the squirrels would be churring. Through the morning until about 10:30 they remained actively foraging, but after that and until about 2:00 p. m., they were rarely seen. This corresponds roughly with my observations (1929, p. 78) and Hamilton's (1939, p. 742) on the red squirrel in the east. The major summer activity period there extends from dawn to about 9:00 a. m., with a marked quiet period in midday. At no time were the pine squirrels seen or heard in the night.

VERTICAL RANGE

Great altitude is probably not directly a controlling element in distribution. That is, there is no evidence to indicate that the lower air pressure nor the more

severe climate of higher altitudes could not be endured by the chickaree, but through the elimination of favorable nesting and feeding areas the squirrels are kept to moderate altitudes The highest point at which I have seen the pine squirrels was in the upper limits of a mature spruce-fir growth in the Brainerd Lake area. This site was at about 11,000 feet. The lowest point at which squirrels were seen was at about 8,500 feet on Devil's Head Peak, southwest of Sedalia. Near Colorado Springs this squirrel occurs (Warren, 1910, p. 187) down to 6,000 feet, a vertical range, roughly between the first and second miles of altitude.

THE FAVORED FORESTS

The lodgepole (*Pinus contorta* var. *Murrayana*) forest is the favored home of the pine squirrel in the Front Range of Colorado, and in these forests it attains its optimum populations. To favor the pine squirrel a stand must be cone-bearing and dense. A dense stand of trees 15 feet high and three inches in diameter will sometimes harbor a few squirrels, whereas an open growth of trees 20 feet by six inches may have none.

Isolated spruces appear to harbor no squirrels. Squirrels are abundant, however, in heavy stands of Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*) and Alpine fir (*Abies lasiocarpa*) or spruce and poplar. Squirrels are found in the magnificent tall fir stands just below timberline, but appear not to invade the areas of stunted growth.

The pine squirrel is absent in the yellow pine (*Pinus ponderosa* var. *scopulorum*) forests where the trees are not greatly mixed in with other conifers. The yellow pine, forming an open growth, with poor protection to a squirrel and with cones of a proportion to discourage feeding, does not seem well suited to the pine squirrel. In only one situation, along the Nederland-Ward highway, in a stand of mixed small yellow pine and lodgepole, did I find one nest and yellow pine cones that had been opened or shucked by the squirrels. On the other hand, it is reported by Cary (1911, p. 69) that in the Escalante Hills in the northwestern corner of the state, this squirrel comes down among the yellow pines at 7,000 feet during the winter. In other sections, he observes, the pine squirrel was found where pockets of balsam and aspen were scattered among the yellow pines.

The limber pine (*Pinus flexilis*) is also of sparse growth habit, though a tree of higher altitudes. Its cones also are robust, but its seeds are frequently eaten by the pine squirrel. On the moraine above the University Camp where the limber pine is abundant, the middens all contain a large number of the limber pine cones, but the squirrels occur only where other trees, (spruce, lodgepole, fir) form dense clumps alongside of which grow limber pines. The limber pine forms a favorite perch tree where it occurs in a feeding area, and middens under limber pines are frequent, though nests in such trees are rare. The open, low, naked branches seem to offer an esteemed place on which to sit and shuck a cone.

The squirrels occur in areas where no free water or snow is available to them in late summer and they must gain adequate amounts from their foods or from precipitation.

FIRE

The pine squirrel population in the Front Range is largely correlated with its most abundant food tree, the lodgepole pine, and the lodgepole in this region is the sequel to fire. When fire sweeps through a lodgepole forest, the chickarees are certainly frequently burned, or at best forced to move on, their food and shelter gone. But beyond this simple and obvious condition there are other factors relating fire, forest, and squirrel.

A fire started July 20 along the railroad between Rollinsville and the Moffet tunnel. It burned quickly uphill to the summit of the ridge where it was brought under control. The fire progressed chiefly along the ground, burning most thoroughly where the lodgepoles were close together. Here the ground cover was completely burned, even to the squirrel middens, and if there were squirrel nests they were fully consumed. Aspens, too, were fully destroyed, but the more scattered and larger yellow pines were little more than base-burned. When I visited the fire the next morning, it was well under control by a C. C. C. unit. One of the boys spoke of seeing chipmunks (possibly both *Eutamias* and *Citellus lataralis*) running around, looking puzzled and helpless. I saw none myself, but a few ants were observed moving over the scorched ground. The survival of the ground squirrels would indicate that the chickarees, where they had tunnels, might occasionally escape burning by retreat to the ground. In this connection it is interesting to note that in 1938, a few days after a 2000-acre fire on the opposite side of the valley, Mr. Rodeck observed fresh squirrel work on cones of the lodgepole.

This 1938 fire was a very hot and completely destructive top fire, but only the tops of the middens were scorched in the area examined. The chickarees seen by Mr. Rodeck may have moved into the burned zone from its margin, or it is possible that they escaped by staying in burrows. It has even been suggested that the chickarees are successful in the lodgepole (to the exclusion of other arboreal squirrels) because of their use of underground tunnels.

One pine squirrel at least escaped the 1939 fire. In the center of the burn was a group of one large and two small lodgepoles, all base burned and with the needles browned, but not actually burned more than 10 feet above the soil. Another tree in the group was carbonized, the needles gone—and in this tree was a very distraught squirrel, haranguing the fire-fighters. It was a thin looking female that obviously was not nursing young. In the same tree, 15 feet above the ground and 8 feet out from the trunk, was an unburned grass nest. Its entry was open, but it was empty. No nest was in the adjacent unburned trees. I spent a half hour in the tree, at the level of the nest, and the squirrel often came close to me, scolding and probably associating me with its calamity. With the shelter of its nest and a food supply in these trees this squirrel might have continued to live in the fire area, though destruction of most of its foraging range made an early move seem the more probable.

A year's sequel to a fire was seen by a 1939 examination of the big Rollinsville burn of 1938. Here was a scene of desolation—the trees scorched (although some retained their dead needles), the ground burned and washed largely to barren

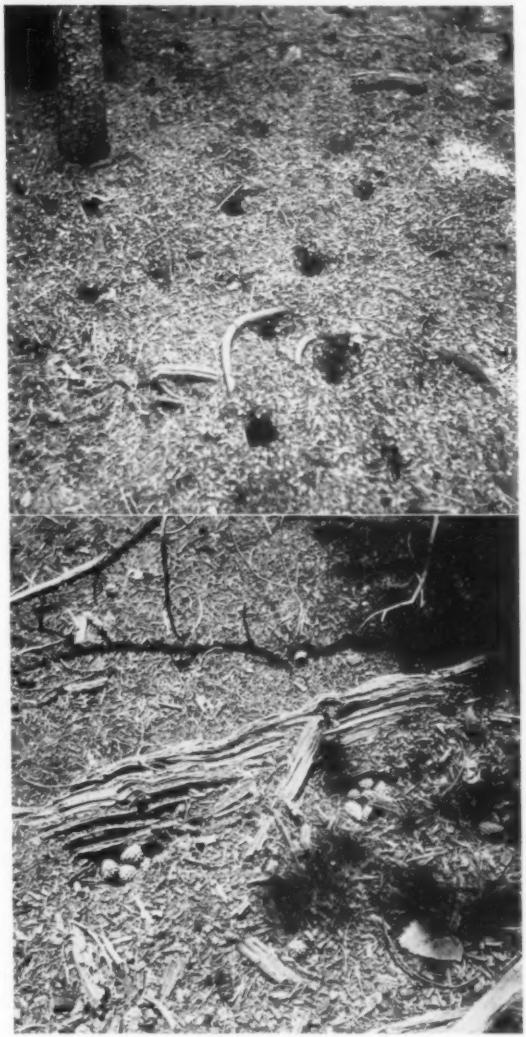

PLATE 5

UPPER: Pine squirrel midden in a spruce and fir forest. The numerous pockets are made in removing stored cones. Boulder Co., Colo., July 14, 1939.

LOWER: Newly harvested lodgepole cones placed in shallow pockets in the ground and left uncovered. Rollinsville, Colo., July 18, 1939.

rock. Lodgepole cones still clung to the trees but were open, their seeds largely scattered. Few ground plants had appeared, these principally roses, bearberry, fire-weed, a willow, false cinquefoil and cowpeas. Of these the perennials were

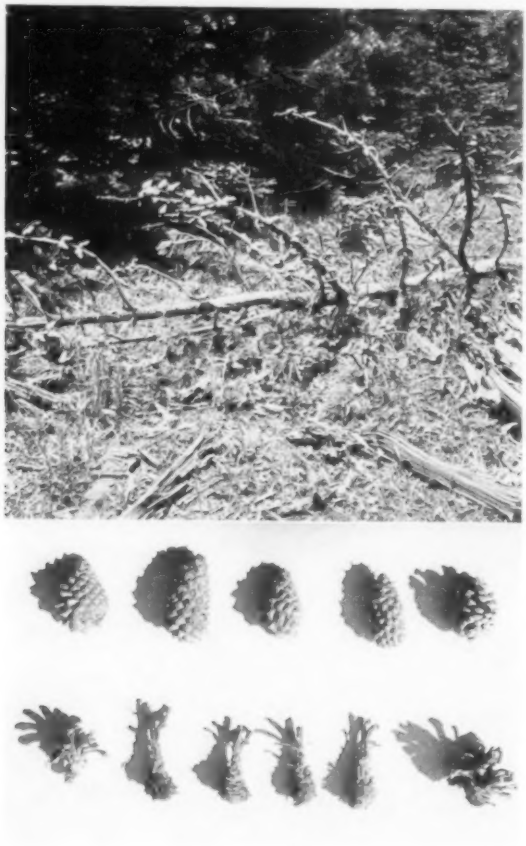

PLATE 6

UPPER: A lodgepole that had fallen some months before being photographed, showing the persistent closure of the cones. Boulder Co., Colo., 1939.

LOWER: Lodgepole pine cones showing varied shape of stored cones (above) and typical shucked cones from a pine squirrel midden.

growing from unburned roots. Somewhat favored as sites for new growth were the squirrel middens. These had been but surface burned, their wet bases resisting the fire and helping to protect the roots of bramble and bearberry, offering good footing for fire-weed. No lodgepole seedlings were seen. No

animals were seen in this old burn except numerous flies and grasshoppers, a robin, and a flock of 6 mountain bluebirds that seemed to be feeding on the grasshoppers, and a flock of about 12 pine siskins, feeding on seeds in the attached cones of the lodgepole.

SPACING

In two areas I had opportunity to become sufficiently familiar with the squirrels and trees to feel that I knew each individual squirrel and nest. One of these areas was a tract of lodgepole forest uphill from Science Lodge, the other a smaller area of lodgepole near Rollinsville.

In the Rollinsville tract, limited by a stream, a meadow and a roadway, the

FIG. 2. Spacing of pine squirrel nests and middens, on a ten-acre plot near Rollinsville, Colo., July 13, 1939. Midden areas are indicated by broken lines; nests by burr patterns.

forest was pure lodgepole, except on the edges where aspen occurred. The pines were three to eight inches in diameter, except at the northern edge where they were somewhat larger. This tract (fig. 2), roughly triangular, contained approximately ten acres. Within this forest I knew of four midden areas, three central and one peripheral. Each of these appeared to have an adult squirrel associated with it, but, though the tract was quietly observed for many hours on several days, never was more than one squirrel seen or heard in any midden area. This observation corresponds with that of Gordon (1936, p. 171) who found each midden area jealously guarded by a single squirrel. A fifth squirrel could not be associated with any known midden or nest. In each of two of the central areas there was one old nest and one new one. In the third, not a single nest could be located although a very ancient nest occur-

red about 50 feet away. The seemingly nestless midden area was marked by many short tunnels, but, though all found were explored, no underground nests could be located. It is possible, of course, that this was a feeding area for a squirrel nesting at a distance. Within this area (30 feet in diameter) was the dead tree elsewhere described, with much of its bark squirrel-removed and here also I watched a squirrel cut down many cones. The other area, at the edge of the stand, had but one nest.

The diameters of the midden areas mentioned were about 100 feet, 40 feet, 40 feet and 30 feet. The areas in the central forest were about 500 feet apart, the peripheral one about 700 feet from the nearest.

On the basis of the presence of five adult squirrels to ten acres there was a population of but one squirrel to two acres, indeed a small census.

In the area above Science Lodge, unmeasured but embracing about 25 acres of lodgepole of somewhat younger growth than the Rollinsville area, I knew of six adult squirrels and four nest-young. Seven nests were found here; only three established middens. There was thus a smaller adult squirrel population than at Rollinsville.

Through observation of many living squirrels in the Front Range, I would estimate that the summer foraging range was in excess of 100 yards.

In general, squirrels were absent in young forests, and in places where growth was open. They were never found more abundant (to judge chiefly by cone debris) than in a mature stand of lodgepole, about 50 feet high, with which were mixed a few spruce and fir. Here shelter and food supplies were excellent and the accumulation of squirrel food debris indicated long tenancy. Large, isolated spruces, though probably possessing adequate resources for one or two squirrels, were not utilized.

NEST GROUPINGS

The pine squirrel, free of communal obligations and with family responsibilities at a minimum, living in an environment where at least in most years food and nest materials are available beyond the possibility of exhaustion, has much leisure time. That some of this is expended in architectural pursuits beyond the main nest seems probable. The rapidity with which mother squirrels moved their young to other nests when the occupied nest was disturbed showed that female squirrels with broods, if not all mature pine squirrels, have reserve nests ready for occupancy.

These squirrels are so unsocial in their behavior it seems unlikely that clustering of nests indicates several families sharing a limited territory, nor are these nests likely to serve as guest houses. Where many nests have been found close together they have been in groups of mature trees, under which large middens occurred. The middens indicate long occupancy of a site; the multiplicity of nests probably the same.

That some of the nests in such clumps are "dummy" nests has been suggested by Long (1940, p. 175), but there is an insinuation of deceit in the word "dummy". It is true that there is a factor of safety, doubtless unconcious, in nest

groupings, in that such a predator as a marten might give his presence away by first investigating an unoccupied nest. Yet by the same mark a nest site becomes increasingly conspicuous with added numbers.

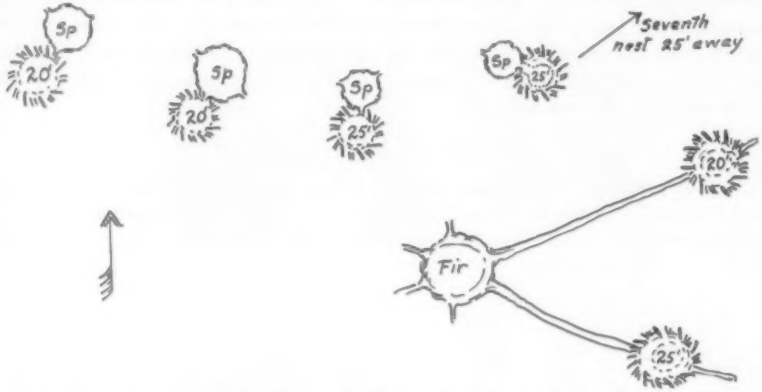

FIG. 3. The grouping of six pine squirrel nests in a cluster of Engelmann spruce and alpine fir. A seventh nest was but 25 feet away. Nearby trees were lodgepole and limber pine. The figures indicate height of nest, in feet.

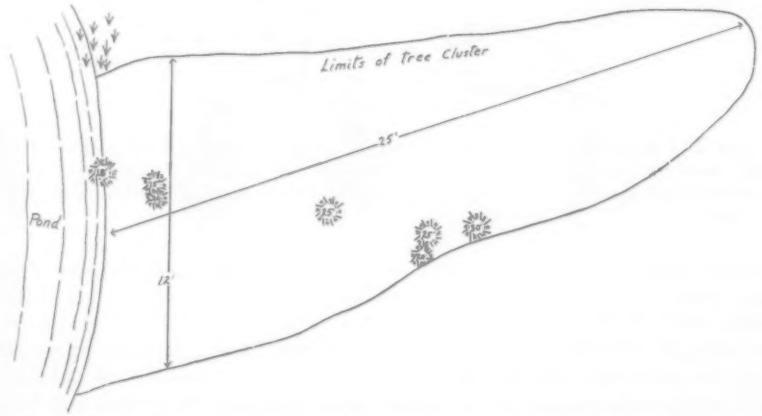

FIG. 4. Spacing of seven pine squirrel nests in a grove of spruce and fir. Moraine above Science Lodge, 1939.

One site where seven nests occurred may be described. In this instance (fig. 3) six nests within a radius of seven feet occupied a group of five spruces and a fir along the trail between Science Lodge and Rock Lake, up on the moraine. Another nest was but 25 feet away in a lodgepole pine. The surrounding forest was in general a fairly open growth, chiefly of lodgepole and limber pines. Of

the seven nests, three were deserted. Since squirrels were not seen at the spot, I can present no information on the significance of the number of nests. Another group (fig. 4) of seven nests in larger trees about a mile from those mentioned above, could not be so readily examined. The clump of trees in which these nests occurred had a maximum diameter of 25 feet and the nests were confined to less than half the area. Two of the nests were in one tree; three within five feet of one another (Plate 10, upper). Four of the nests were taken down. Each might have been occupied.

RESTRICTION TO OUTSIDE NESTS

Activity through the coldest months makes a warm, dry nest an essential and Fremont's chickaree constructs an adequate nest. Underground nests are unknown in this region, because perhaps of the lack of dry deep soil. The

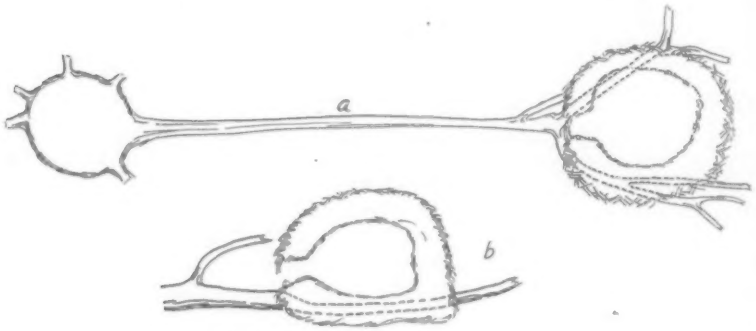

FIG. 5. Typical pine squirrel nest at 20 feet in a lodgepole pine. *a*. the position in the fork, three feet out from the trunk. *b*. elevation of the same nest. The lining was of shredded bark, the base, walls and thatch of grass. Rainbow Creek, Boulder, Colo., July 6, 1939.

relative absence of natural tree cavities and hollowed stumps in the area of the pine squirrel is, I presume, the direct reason for the nests almost universally being constructed on tree limbs. Were tree cavities available, it is almost certain that the pine squirrels would be found to occupy them. Rotting stumps and logs of considerable age and variety are characteristic of much of the southern range of the red squirrel, and that species makes abundant use of them for shelter and storage. In the pine squirrel's range, however, such trees as do reach the ground decompose quickly and are not likely to provide suitable shelter.

On but one occasion (June 18) did I find a squirrel in a hollow log and the reason for that occurrence was not obvious. The log was a lodgepole, lying in an open stand. The squirrel was a lactating female. No nest or food was in the log.

Nests in human habitations are doubtless as common among the pine squirrels as the red. In Boulder County I heard of their occasionally entering cabins

and occupying them, but this habit is more characteristic of the neighboring pack rat (*Neotoma*). Though not in any sense primitive, cabin occupancy may be indicative that hollow trees, to which they are analogous, would be used if available.

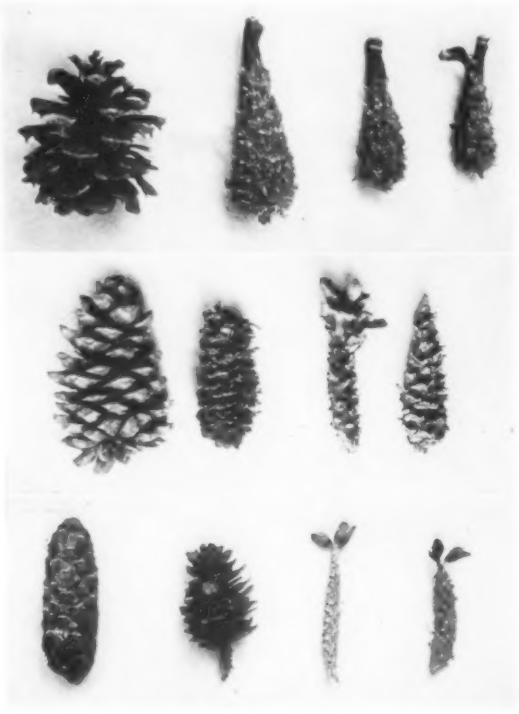

PLATE 7

Upper: Yellow pine cones: Left: a cone naturally opened, with seeds dispersed. Others: variation in pine squirrels' shucking results.

Middle: Limber pine cones: Left: air-dried and opened. Others: shucked by pine squirrels.

Lower: Engelmaan Spruce cones: Left: as stored. Others: shucked by pine squirrels.

In the short period of study, notes were made concerning 48 nests. About half of them were examined closely enough to be handled. Certain generalizations may be excepted or supported by details below.

Nests were commonly (18) found in lodgepole pines, as would be expected, since the greater part of the squirrels' local range is in the lodgepole forests. Almost as many (16), however, were found in spruces. Seven were seen in fir trees, but only a single nest in a limber pine. The more open growth habit of

the limber pine affords less protection to the squirrels and it is presumably for this reason that the trees are not commonly used.

PLATE 8

UPPER: Staminate conules of the lodgepole, a frequent summer food of pine squirrel. June 19, 1939.

LOWER: Staminate conules of the lodgepole. Left: cluster as harvested by the pine squirrel. Others: twigs left after the conules were eaten, by a pine squirrel.

The nests are not found in very young trees. In a stand where all the trees are young, food is scarce and the squirrels are not resident. In older stands the more mature trees offer safer sites to the squirrels. Nests high in the crowns of mature trees would ordinarily go unobserved so that conclusions indicating

usual height of the nests must be admitted as probably erring on the low side, although in one group of seven nests the highest was at 30 feet when seemingly equally choice sites were available at double this. The mean height of nests observed was 20 feet, although others were at from 8 to 60 feet. Few nests occurred lower than 15 or over 30 feet. Among the low records were: one at 8 feet in a small leaning alpine fir, in a swampy area; one at 10 feet in a small dead spruce crowded by two living spruces. Two nests seen at 50 and 60 feet respectively were in large spruces exceeding 100 feet in height.

The nest is usually placed where it is firmly supported and as well protected from the weather as the site permits. This means that the outermost section of the branches is avoided, the extremity of the crown ordinarily unused. Diameters of the trunk, either of the tree at its base or at the level of the nest are, I believe, of no significance. Nests in my observation are most commonly in contact with the trunk, straddling one or more limb bases, though Cary (1911, p. 70) found them "usually well out from the main trunk". Of 36 nests in which the position was described, eleven were at a distance of from one to four feet from the trunk, a single one at eight feet. One nest was in a broken lodgepole top, cradled between seven leaders. Four nests were in bunches of mistletoe or witches broom.

The nest itself is roughly globular, sometimes flattened above and below but occasionally deeper than broad. Its horizontal diameter varies from 11 to 18 inches. Inside is a cavity, four to five inches in diameter, and leading to this from the outside is a single passage the diameter of the squirrel's body. The doorway is sometimes concealed by a section of the thatch hanging over the entry. It may be that when a squirrel leaves the nest in a leisurely manner this hanging door is arranged as a screen, for in some nests I needed to search for the entry. However, when I had certainly frightened the squirrel from its nest the entry was conspicuous. This doorway may face any point of the compass, face the trunk or away from it. I presume that it is always toward the best branch highway.

The nest has no platform of sticks supplied by the squirrel, although in the base of the nest or in the crotch in which it may be placed there is sometimes an accumulation of pine needles, rarely broad leaves and plant fibers which the squirrel possibly placed there.

The nests are most commonly of grass, which is abundant enough in typical squirrel areas. With this there rarely appear a few pine needles and aspen leaves. The grass on the outside is not comminuted but that lining the interior always is well shredded and soft. Cary's (1911, p. 70) description of the nests as "of pine and spruce needles and fine strips of bark" is scarcely typical of my findings.

Two nests of distinctly different makeup were found, and these occurred in a wet spruce area, of a type not occupying large areas in the mountains. These nests were lined with shredded spruce bark and a little moss (Plate 10, lower). In the vicinity of the nests there was little grass; in the vicinity of most grass nests, little moss.

One nest more varied than others, perhaps because located near a roadway,

was mainly of grass but with some string admixed. It was lined with fluffed string, grass, and many breast feathers of a robin. There was also the end of a squirrel's tail, including a centimeter of the vertebral column.

Minor amounts of extraneous matter are occasionally found in nests—tufts of squirrel hair, parasites, and once three small snail shells that may have come in with some sedges incorporated into the nest. Fecal material was not seen in the nests. A white rag was caught on the trunk of one tree just below a nest containing young. Similar conditions are reported by another (see Social Status).

That nests are sometimes built on the platforms resulting from old deserted nests was indicated by one nest in which stratification of the base indicated that two or more earlier nests had been at this site. I have not found one built on an old bird's nest.

Just as the squirrels are independent of streams and lakes, so of course are placements of the nests. In one instance I did find a nest directly over the water, in a fir at the edge of a pond, but if anything this was a disadvantageous position since ready escape was limited on the water side.

The life of a nest extends over several seasons. Of two nests occurring near one cabin where they had been regularly observed by Mr. Rodeck, one was in its fourth year, the other in its first. Eventually a nest is deserted and becomes a sodden flat-topped mass that may serve as a feeding platform. Some are blown out of place and, of course, then deserted.

The nest of the pine squirrel may be said to differ from that of the eastern red squirrel only in its greater limitation to type. The red squirrel, usually with greater resources, is likely to have a more diversified nest. A variety of broad leaves, of bark, of nesting sites in hollow trees, stone walls, etc., gives it an advantage not enjoyed by the squirrels in the mountains of Colorado. Outside nests of the red squirrel are rare in places where broadleaved trees provide abundant nest cavities. The underground nest, occasional in the East, was unobserved in the home of the pine squirrel.

The time at which nests are started cannot be stated on the basis of a study involving but the tenth part of a year. Apparently fresh starts of nests were found on July 3 and July 11, but at no time did I witness nest building activities.

A LIMITED DIET

The seeds of the lodgepole pine, limber pine, Englemann and blue spruces, Douglas fir (*Pseudotsuga taxifolia*) and Alpine fir and the lodgepole staminate flowers formed virtually the only foods of the squirrels during the early summer of 1939. Seeds of the yellow pine must be listed as a food available on the periphery of the range and not extensively utilized. The bark of the lodgepole fits somewhere in the picture as attested below, probably as a winter or early spring supplement to diet. In less dry years fungi must well supplement this as affirmed by other observers. Two old dried fungi, (a *Russula* and a *Polyporus*), relics of other years, were recovered on sites that suggested squirrel storage,

PLATE 9

UPPER: Branch of a lodgepole from which bark was removed by a pine squirrel. Note subsequent healing. Rollinsville, July 18, 1939.

LOWER: Trunk of a dead lodgepole from which squirrels have removed a patch of bark. Rollinsville, July 18, 1939.

The presence of the bones on the middens may account for the frequency of hare scats on the mounds, for hares also gnaw at bones. An equally tenable explanation, however, might be that the middens, by reason of squirrel activity and size, may be pleasant resting places in time of light snow.

BARKING OF TREES

The red squirrel of the east barks a variety of trees for nest material and in feeding activities, but the pine squirrel, with a less varied forest at his disposal, gives less evidence of such injury to living trees or utilization of dead trees. Observed barking by the pine squirrel was limited to removal of bark in the upper sections of lodgepole pines and removal of bark of a dead lodgepole.

Four instances of the removal of living bark were observed. Three of these were in nest trees, within a few feet of the nests; the other in a tree adjacent to one supporting a nest. There is no reason to presume, however, that barking is confined to the vicinity of nests, since I never ascended a tree to the crown unless a nest was first seen or suspected. In each of the trees the cutting dated back at least to early spring since bark healing was everywhere evident. On one tree about 60 square inches of bark had been removed near the nest—chiefly in scattered patches about two inches in diameter. In the tree lacking a nest, the removal had been extensive. Such work, though similar to porcupine injury is readily distinguished by the size of the teeth marks. Sheldon (1932, p. 199) records that the red squirrel (*T. h. hudsonicus*) living in lodgepole forests of British Columbia had the "tender, sweet inner bark" of the lodgepole as the *chief summer diet*. He writes, "I observed them often gnawing away the outside bark to reach the inner layer and in many cases they had ringed the tree near the top, thus accounting for many dead tops." Summer removal of Douglas fir and of oak bark, with killing of the tops, presumably by the Douglas chickaree, is reported by Moore (1940, p. 11).

Removal of a large amount of bark from a dead tree (Plate 3, lower) was observed but once. Here, in a dense stand of small lodgepole, a single dead tree, six inches in diameter, had most of the bark removed to a height of 15 feet. The many tooth marks were practically all horizontal. The absence of loose bark on the ground near the tree would indicate that the larger fibers, at least, had been used in nest construction. The stand was occupied by squirrels, although a careful search of the trees and the ground in the vicinity failed to reveal a nest nearer than some 400 feet away. The virtually complete absence of grass in the dense stand in which the stripped tree occurred, suggests a reason for resorting to bark fibers, had a nest been required. Search for bark insects may, of course, have been the reason of the barking.

The significance of the bark as a food and bark as an emergency nest material may be great to the individual squirrel, but in Colorado the effect on the forest must be negligible in both instances since so little of either type of work was observed.

THE MIDDEN

The midden pile of cone bracts and cores is the center of the pine squirrel's domain. By it one knows his presence, the relative length of his occupancy

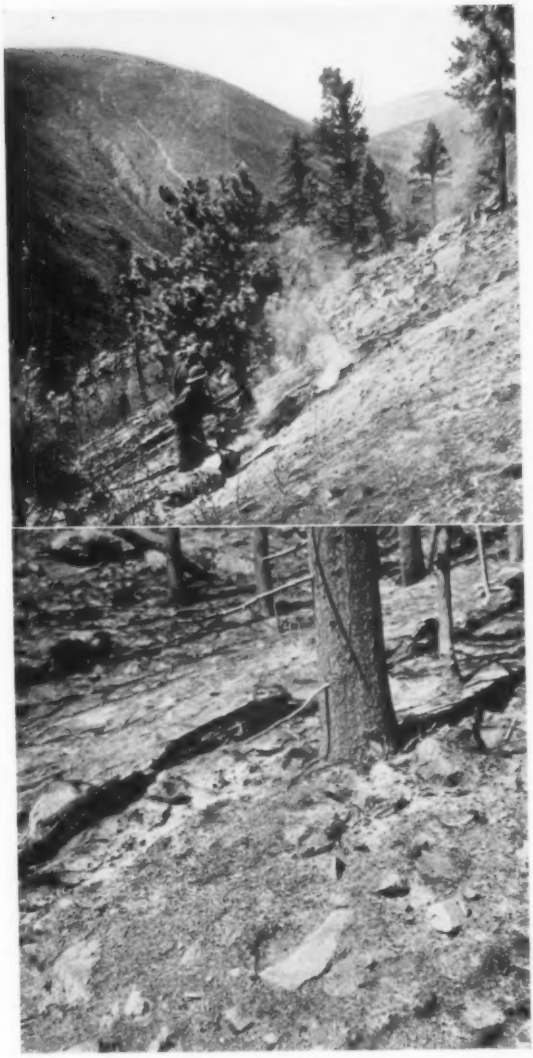

PLATE 11

UPPER: Fighting the Rollinsville Fire. Note that in the open growth on this south facing slope many trees escaped with little injury. On the far slope is the site of the 2000-acre 1938 Rollinsville fire, in which a dense lodgepole stand was fully destroyed. Boulder Co., Colo., July 21, 1939.

LOWER: Scorched squirrel midden from the 1938 Rollinsville fire. All trees in this area are dead. July 11, 1939.

PLATE 12

UPPER: Lodgepoles about four hours after the peak of the fire. Note the live pine squirrel to the right of the lower part of the central trunk. Rollinsville, Colo., July 21, 1939.

LOWER: An unburned squirrel's nest, which passed through the 1939 Rollinsville fire. The photograph is taken outward from the supporting trunk. July 21, 1939.

of the site, and something of his habits. Here he feeds, drags old bones to gnaw on them, buries a portion of his cone harvest. It is his gatepost, easily dug, easily located. Other rodents do not dig in it. It is a testimony of the squirrel's localization and of the monotony of his diet. The relatives of this squirrel (*Tamiasciurus douglassi* and *T. hudsonicus*) in the west and to the north, where they occupy similar habitats, leave records like that of the pine squirrel, but the red squirrel of the eastern states, leaves lesser piles of debris.

Middens are usually centered about a tree or cluster of trees, about a stump or log. The squirrel secures a large share of his cones from the ground, just before feeding. These may have been freshly cut, several at a time, have been on the surface for several days, or have been buried a matter of months. The squirrel commonly carries his food to a low perch, sometimes a log, sometimes a stump, most frequently a limb, from which he has a clear view and ready access to safety, and here, while eating, drops his trash.

Pine squirrel nests always have some midden below them for the squirrels frequently feed near the nest, but many middens have no nests in the immediate vicinity.

Middens, of course, vary from the litter made from consumption of seeds from a single cone to a great accumulation of years. The size of some middens would indicate the accumulation during generations of squirrels and these piles may, in fact, be almost as old as the forest in which they occur. Concentrated middens forming mounds are the result of restriction of suitable feeding perches. Where many good perches occur the midden is likely to be diffused. Well defined middens of large size were found. One of these measured 35 feet by 10 feet and was evenly spread between twenty-four trees and six logs. Another was about 25 feet in diameter and was 18 inches deep. Middens lack stratification probably both because they are constantly accumulating with the same sort of material and because the squirrel's frequent digging activities disturb much of the structure.

The structure of one midden dissected and described was typical of the others. This midden measured 18 inches deep down to the glacial till on which it rested. The upper 3 inches of it was of dry scales and cone cores; the lower 15 inches was damp and humus like, with the identity of the source material largely obscured. This section was interwoven with rootlets and white material resembling, if not actually, mycelial threads of fungi. Other middens showed tunnels or plugs of cone scales occupying old tunnel sites. Cone storage in middens is irregular, by no means constant.

Do middens serve as germinating beds? Seemingly not. Examination of middens in a year-old fire site did show sprouting blueberry, roses, and other deeply rooted plants, but no conifer seedlings. In unburned areas an occasional pyrola is seen in a midden, but usually they are kept clean. Such cones as are buried in middens are probably kept too cool to germinate, or, if not eaten within a year or two, rot, as recovered cones indicate.

FEEDING

The feeding activities of the pine squirrel in early summer were largely devoted to cutting of cones for immediate consumption and for storage, the excavation

of stored cones, the cutting of the staminate conules of the lodgepole, and a promiscuous amount of foraging with results that were never evident to me. They are seen feeding at all times of the day in which they are active.

No excessive amount of agility is required in reaching the usual foods, since the flowers and fruits of the pine, fir, and spruce are carried on relatively sturdy branches. Cones and flowers are sometimes eaten from the same perch from which the cutting was done, sometimes allowed to fall, later recovered, and carried to an elevated feeding site. During cutting, the squirrels occasionally hang head down to reach cones below them. I have watched a squirrel hanging freely by his hind feet, drop his own length to a lower limb, with cone in mouth.

The noise made by their teeth clipping off the cones' scales to reach the seeds is audible for a considerable distance on a quiet day, and frequently leads to the discovery of the squirrel. At such times, if not too closely approached, the squirrel is likely to finish work on the cone before giving his attention to the observer. One squirrel was timed to shuck and feed from three cones in four and one-half minutes.

I saw no squirrel that had pitched up his face in cone cutting or feeding, though no doubt under some circumstances they do become soiled.

THE HARVEST AND ITS STORAGE

Freshly cut lodgepole cones were found in open pockets in the middens as early as June 22. These were of the previous season's growth. For an hour, from 5:30 p. m. on July 17, I watched an adult male squirrel cut cones in a thick growth of young lodgepoles. The squirrel moved about among the trees (few bore cones) and he spent much time scolding but did not come down to earth while I watched. The hour's work resulted in a cut of only 55 cones, 25 from two adjacent trees, 30 from another, 30 feet away. Most of the cones were cut "clean"—that is without any branch; but others, sometimes two or three in a cluster, had six inches or more of twig attached. Some of the cones were freed of attached twigs after being cut with them, but before being dropped. One tree was considerably defoliated by the cutting but the forest as a whole obviously does not suffer. The cones were left on the surface of the ground overnight.

That cones may thus be left on the ground for a considerable time is indicated by a find, July 3, of some 50 lodgepole cones, two to three in a cluster, scattered beneath a tree from which, to judge by appearances, they had been cut more than a week earlier. It is possible, of course, that this was waste cutting or that an accident befell the harvester before the cones were put away, but it is well known that eastern red squirrels often leave their harvest ungathered for several days.

Cones cut as early as June 22, may be placed in numerous pockets in the forest floor or small midden heaps, where they are sometimes left exposed for several days. Typically, these pockets are numerous in a small area, and each may contain 6 to 30 or more cones, tightly packed. A store of 125 newly cut small lodgepole cones was found in one midden July 18. Of these, 23 were in

one pocket. Storage in large middens appears to be exceptional. I have not observed storage by piling cones in the open, as has been reported by others. At one site where there were piles of slashings the squirrels buried the cones in ground pockets under the brush.

Cone storage has only been observed within a radius of 75 feet of nest trees. I have observed a pine squirrel carry a cone 150 feet to store it.

There is much evidence that when a cache is opened the squirrel may continue to use food from the pocket until it is empty, for around an opened pocket there are usually many equally weathered cones and bracts; in one instance, the remnants of 80 cones.

Cone storage underground, particularly in the areas of spruce and fir, must be of significance in a lean year in guarding for the harvester a personal food reserve. Here, with the protection of the ground moisture, the cones do not open and scatter their seed, the cool earth retards decay and, following a top-fire, the buried food might prove adequate reserve for the contingency of the moment. At other times storage of lodgepole cones seems of little importance since the seeds are not scattered as in most of the conifers. The burial of spruce and fir cones, however, is always important, for their seeds are dispersed early in life.

No large caches of cones were found as reported by Yaeger (1937, p. 191) for Michigan red squirrels. His record of seven bushels of cones in one spot is far above any record of mine. Yaeger's observations were made in November—four months later than most of my field work, and in this time there is opportunity for a great deal of harvest. Yaeger testifies too that study of the same area a year later disclosed no fresh caches or evidence of cone piling, a fact attributed to failure of the cone crop.

The significance of chickaree-stored cones as sources of seed for forestry is belittled by Moore (1940, p. 11) who observes that although these cones almost invariably have a high seed count, seed collectors in the Douglas fir region find it more profitable to do their own picking than to rely on caches.

Fungi are known to be stored by the pine squirrels in wet years but the season of my study was exceptionally dry and no fresh fungi were seen. Two old dried mushrooms were found where squirrels may have left them, one on the surface of a midden, one in a tree from whence it was shaken with a squirrel's nest.

REPRODUCTION

No sexual activities were observed among the squirrels, although occasional scamperings about the ground may, of course, have been sexual in nature rather than defense of territory. About September 1, 1919, I observed two pine squirrels in coitus in this same region. The period of major sexual activity is doubtless in late winter and early spring.

A gravid female was collected May 17, at 8000 feet, in Utah, by Long (1940, p. 175).

Nursing females were collected or observed from June 18 to July 17, almost

the length of the field season. Two females collected July 5 and 6 contained no embryos, but were nursing. A litter of four was found in a nest July 3. These were 185 mm long, blind, but well furred. Two young were obtained in a nest July 14. These, unmeasured, were somewhat smaller, scantily haired.

A tame female red squirrel (*T. h. loquax*) less than one year old, allowed access to a house by an informant, Miss Margaret Gray, of Oswego, New York, came to the house door on March 29, after being outdoors for two days, rushed to her cage, and sometime in the next few hours gave birth to a litter. This particular unusual observation of an unnatural circumstance would indicate that a female under normal conditions probably leaves her young in a nest with which she is long familiar; probably not one shared with a male. Parturition in the first year is apparently normal to the species.

The mammae, as in the red squirrel, are two thoracic and two inguinal on each side.

As noted elsewhere, the young encountered were richly supplied with fleas.

BEHAVIOR NEAR THE BROOD NEST

An adult female (July 3, 8:15 a. m.), scolded me for one minute from a tree 72 feet from her nest which contained young. She then came down to the ground where she foraged quietly. At 8:22, having got near her nest, she dashed up a tree and again scolded. She came yet nearer, through a tree highway, and continued to scold. When within 20 feet of me and in clear view, she settled down to regular scolding. Twice she dashed to the ground, on the second ascent carrying a cone on which she fed from at a height of five feet. This was twice repeated before she stopped again to express herself. A short dash around in the trees was followed by descent to the ground, over which she traveled for 100 feet. Her scolding was then answered by another nearby squirrel; also scolding. The first squirrel then churred while the second continued to scold. A man passing between the two occasioned both to scold him for two minutes, after which there was silence. The female squirrel moved to her nest tree and entered her nest. At this point I moved over to the nest tree and started to climb The mother left the nest and the tree well before I attained the level of the nest, but when my head was opposite the entrance the squirrel returned over the branch highway to a position high in the nest tree and descended to within four feet of my hand, and there scolded vigorously. As I reached in the nest she came down to its roof then, losing courage, dashed to another tree. Two minutes after I had reached the ground the mother returned and searched over the nest but appeared reluctant to enter. Five minutes later she entered it, came out carrying one young, descended to the ground where she stopped a half minute to readjust her load and carried it 40 feet to another nest well concealed in the dense crown of another lodgepole pine. Three more young were quickly transferred to the other nest. All four had been removed in five minutes, efficiently and silently. On each trip the same general route was followed. After the last of the litter had been moved, the mother returned to the first nest, looked through it at length, then came out and watched

me, came close, returned to examine the nest, and then moved silently away from both nests. Not until eight minutes passed did she return to the nest containing the young.

The nest to which the young had been transferred was examined the following day and still contained four blind but furred young. The mother remained within one to four feet of me while I removed one of the young to the ground. After it had been photographed, I placed it in clear sight on a low stump, then moved away, hoping the mother would quickly remove it. Since in ten minutes she had made no move to do so I took it back to the nest where the mother had remained. One week later both nests were examined and found empty. No other nest was found and in a full hour's wait no other squirrel was seen or heard closer than 400 feet.

Another instance of maternal care was observed. In mid July, a nest at 15 feet in a broken-topped spruce was pushed down and found to contain two very small young. I placed them on the ground near me and almost immediately the mother squirrel, which had not been observed before, came down the nearest tree trunk and approached to within five feet of me, but seemed to lack courage to come nearer. I then placed one of the young at the foot of the nest tree. In a moment the mother came down, picked it up in the manner usual to tree squirrels, and carried it up to where the nest had been. She seemed disconcerted to find it missing, but in a few moments made a short leap to another tree, descended it, ran 40 feet over the ground and ascended a tall tree where there probably was a nest. The other baby was placed where the first had been picked up and the mother came and got this one also, although I was but six feet away. She did not go up the old nest tree this time, but went directly to the tree where the first young had been left. She was not seen again.

HUMMINGBIRD AND SQUIRREL

On the occasion just narrated, when I had removed two baby squirrels from their nest, the distraught mother scolded loudly from a perch 35 feet up a tree. At the time I was occupied collecting parasites from the young animals, but was surprised to have a broad-tailed hummingbird come within four feet of me and, poised in the air, examine the proceedings for several seconds. The bird then moved up to a position just in front of the scolding squirrel and remained poised in front of the animal for at least a full minute. The hummer moved forward to within ten inches of the squirrel's nose but the squirrel, probably too much disturbed by the situation of her young, seemed almost to ignore the bird, although she once appeared to make a fast thrust at the hummer when it was closest. Later when the squirrel was up in a tree carrying one of its young, a hummingbird again approached it closely and chirped, but the squirrel paid no attention despite the annoyance.

LACK OF COMPETITION

Within that section of the pine squirrel's range where I studied, large predatory birds appeared to be rare and no evidence was secured relating to avian predators.

Conspicuous in the habitat of the pine squirrel are Rocky Mountain jays, long-crested jays and, high up, Clark's nutcrackers. I have watched all of these when squirrels were around, but there seemed a complete lack of mutual interest. Hermit thrushes have also been seen close to the squirrels without either species seeming to note the presence of the other. Earlier in the year, when more young birds or eggs were in nests, other conditions may prevail.

Golden-mantled ground squirrels and chipmunks frequently share territory in common with the chickaree but do not compete for nesting sites and appear not to compete for food, except where it is put out for them by man.

Where their territories coincide the red squirrel is sometimes seen fighting with or pursuing gray and fox squirrels, which it is supposed to dispossess, but the pine squirrel has no similar competitors. The red squirrel is victimized on occasion by birds of varied species that steal from his stores, but the pine squirrel stores little other than tree cones and fungi, and doubtless finds few who would rob him of these.

PARASITES AND ASSOCIATES

No exception to the rule that mammals inhabiting well built semi-permanent nests are supplied with a variety of external parasites, the pine squirrel nevertheless appears little troubled with them. Three adults collected appeared free of these guests and none were especially heavily infested, but all fresh nests appeared colonized and young squirrels in the nests invariably shared several large fleas. The heaviest infestation found on an adult was five fleas and one tick.

Fleas were found on adults, on young in the nest, and in empty nests. Dr. H. E. Ewing has identified these for me as *Opisocrostis* sp; *Orchopeas caden*s (Jord); and *Megarthroglossus procus* J. and R.

Ticks were recovered from two adult squirrels. One of these was attached to an ear, the other was free. These were not identified as to species.

Sucking lice were numerous in many nests but were not observed on adults. These Dr. Ewing has identified as *Euhaemogamasus* sp.

A spider was found within one nest, where it may possibly be commensal.

Three shells of the snail *Menetus exacuous lenticulars* (Lea), identified for me by Mr. Rodeck, were found in a nest where I presume they were carried accidentally with grasses and sedges from the margin of a pond at the foot of the nest tree.

SOCIAL STATUS

The red squirrel and the pine squirrel are generally considered untamable and rugged individualists in work and play. The former trait is in part belied by a half-dozen animals that I have known that were tame enough to permit stroking, and the latter by a very interesting observation conveyed to me by Miss Margaret Gray. She noted that in the autumn the red squirrels near her house carried soft old cloth up to their nests for lining. Two members of her family observed *two* squirrels moving a piece of cloth up the tree towards their

nest. While one went ahead and pulled, the other stayed below and loosened any shred that caught on the bark. This same informant tells me of one pair (apparently the same) allowing as many as three other red squirrels to come to a feeding in their territory, without fighting. Even nuthatches were sometimes allowed. Possibly such an abundance of food conditioned the squirrels' reflexes!

Injuries that might have been the resultant of fighting were not seen, except for one lacerated and healed ear.

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TERRITORIALITY AND HOME RANGE CONCEPTS AS APPLIED TO MAMMALS

By William Henry Burt

TERRITORIALITY

The behavioristic trait manifested by a display of property ownership—a defense of certain positions or things—reaches its highest development in the human species. Man considers it his inherent right to own property either as an individual or as a member of a society or both. Further, he is ever ready to protect that property against aggressors, even to the extent at times of sacrificing his own life if necessary. That this behavioristic pattern is not peculiar to man, but is a fundamental characteristic of animals in general, has been shown for diverse animal groups. (For an excellent historical account and summary on territoriality, with fairly complete bibliography, the reader is referred to a paper by Mrs. Nice, 1941). It does not necessarily follow that this trait is found in all animals, nor that it is developed to the same degree in those that are known to possess it, but its wide distribution among the vertebrates (see Evans, L. T., 1938, for reptiles), and even in some of the invertebrates, lends support to the theory that it is a basic characteristic of animals and that the potentialities are there whether the particular animal in question displays the characteristic. Heape (1931, p. 74) went so far as to say:

"Thus, although the matter is often an intricate one, and the rights of territory somewhat involved, there can, I think, be no question that territorial rights are established rights amongst the majority of species of animals. There can be no doubt that the desire for acquisition of a definite territorial area, the determination to hold it by fighting if necessary, and the recognition of individual as well as tribal territorial rights by others, are dominant characteristics in all animals. In fact, it may be held that the recognition of territorial rights, one of the most significant attributes of civilization, was not evolved by man, but has ever been an inherent factor in the life history of all animals."

Undoubtedly significant is the fact that the more we study the detailed behavior of animals, the larger is the list of kinds known to display some sort of territoriality. There have been many definitions to describe the territory of different animals under varying circumstances. The best and simplest of these, in my mind, is by Noble (1939); "territory is any defended area." Noble's definition may be modified to fit any special case, yet it is all-inclusive and to the point. Territory should not be confused with "home range"—an entirely different concept that will be treated more fully later.

The territoriality concept is not a new one (see Nice, 1941). It has been only in the last twenty years, however, that it has been developed and brought to the front as an important biological phenomenon in the lower animals. Howard's book "Territory in Bird Life" (1920) stimulated a large group of workers, chiefly in the field of ornithology, and there has hardly been a bird life-history study since that has not touched on this phase of their behavior.

In the field of mammals, much less critical work has been done, but many of the older naturalists certainly were aware of this behavior pattern even though they did not speak of it in modern terms. Hearne (1795) apparently was thinking of property rights (territoriality) when he wrote about the beaver as

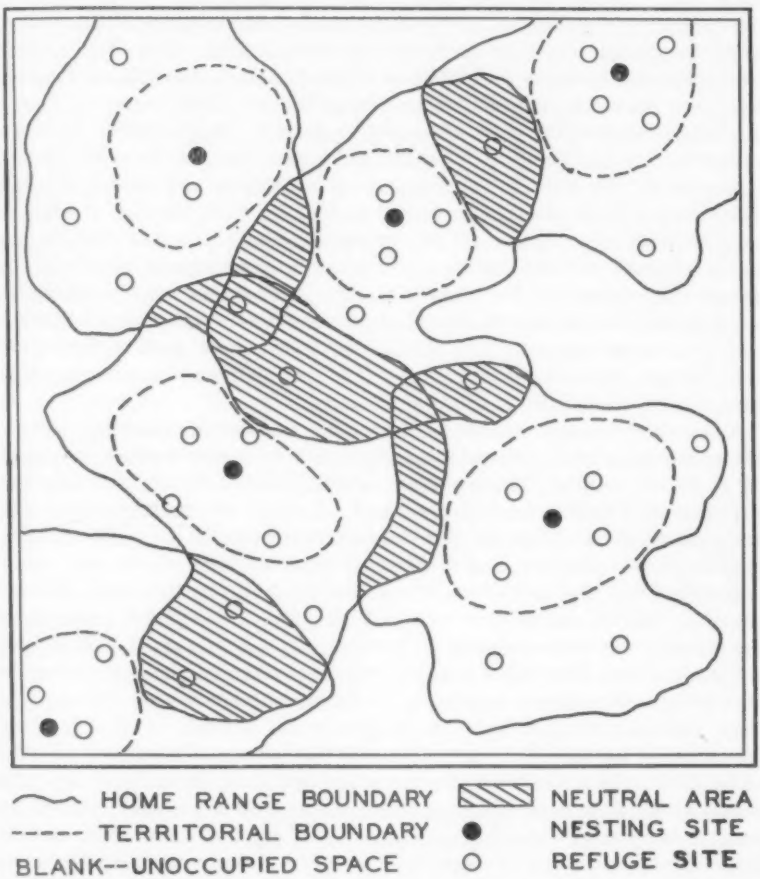

FIG. 1. Theoretical quadrat with six occupants of the same species and sex, showing territory and home range concepts as presented in text.

follows: "I have seen a large beaver house built in a small island, that had near a dozen houses under one roof; and, two or three of these only excepted, none of them had any communication with each other but by water. As there were beavers enough to inhabit each apartment, it is more than probable that each family knew its own, and always entered at their own door without having any

further connection with their neighbors than a friendly intercourse" (in Morgan, 1868, pp. 308–309). Morgan (*op. cit.*, pp. 134–135), also writing of the beaver, made the following observation; "a beaver family consists of a male and female, and their offspring of the first and second years, or, more properly, under two years old. . . . When the first litter attains the age of two years, and in the third summer after their birth, they are sent out from the parent lodge." Morgan's observation was later confirmed by Bradt (1938). The works of Seton are replete with instances in the lives of different animals that indicate territorial behavior. In the introduction to his "Lives" Seton (1909) states "In the idea of a home region is the germ of territorial rights." Heape (1931) devotes an entire chapter to "territory." Although he uses the term more loosely than I propose to, (he includes home ranges of individuals and feeding ranges of tribes or colonies of animals), he carries through his work the idea of defense of an area either by an individual or a group of individuals. Not only this, but he draws heavily on the literature in various fields to support his thesis. Although the evidence set forth by Seton, Heape, and other early naturalists is of a general nature, mostly garnered from reports by others, it cannot be brushed aside in a casual manner. The old time naturalists were good observers, and, even though their techniques were not as refined as those of present day biologists, there is much truth in what they wrote.

A few fairly recent published observations on specific mammals serve to strengthen many of the general statements made by earlier workers. In speaking of the red squirrel (*Tamiasciurus*), Klugh (1927, p. 28) writes; "The sense of ownership seems to be well developed. Both of the squirrels which have made the maple in my garden their headquarters apparently regarded this tree as their private property, and drove away other squirrels which came into it. It is quite likely that in this case it was not the tree, but the stores that were arranged about it, which they were defending." Clarke (1939) made similar observations on the same species. In raising wild mice of the genus *Peromyscus* in the laboratory, Dice (1929, p. 124) found that "when mice are placed together for mating or to conserve cage space it sometimes happens that fighting takes place, especially at first, and sometimes a mouse is killed. . . . Nearly always the mouse at home in the cage will attack the presumed intruder." Further on he states, "However, when the young are first born, the male, or any other female in the same cage, is driven out of the nest by the mother, who fiercely protects her young." Similarly, Grange (1932, pp. 4–5) noted that snowshoe hares (*Lepus americanus*) in captivity "showed a definite partiality for certain spots and corners to which they became accustomed" and that "the female would not allow the male in her territory (cage) during late pregnancy and the males themselves were quarrelsome during the breeding season."

Errington (1939) has found what he terms "intraspecific strife" in wild muskrats (*Ondatra*). Much fighting takes place when marshes become overcrowded, especially in fall and winter during readjustment of populations. "But when invader meets resident in the tunnel system of one of [the] last lodges to be used in a dry marsh, conflict may be indeed savage." Gordon (1936) observed def-

inite territories in the western red squirrels (*Tamiasciurus fremonti* and *T. douglasii*) during their food gathering activities. He also performed a neat experiment with marked golden mantled squirrels (*Citellus lateralis chysodeirus*) by placing an abundance of food at the home of a female. This food supply attracted others of the same species. To quote Gordon: "she did her best to drive away the others. Some of her sallies were only short, but others were long and tortuous. There were rather definite limits, usually not more than 100 feet from the pile, beyond which she would not extend her pursuit. In spite of the vigor and the number of her chases (one day she made nearly 60 in about 6 hours) she never succeeded in keeping the other animals away." This individual was overpowered by numbers, but, nevertheless, she was using all her strength to defend her own log pile. To my knowledge, this is the best observation to have been published on territorial behavior in mammals. I have observed a similar situation (Burt, 1940, p. 45) in the eastern chipmunk (*Tamias*). An old female was watched fairly closely during two summers. Having marked her, I was certain of her identity. "Although other chipmunks often invaded her territory, she invariably drove them away [if she happened to be present at the time]. Her protected area was about fifty yards in radius; beyond this fifty-yard limit around her nesting site she was not concerned. Her foraging range (*i.e.*, home range) was considerably greater than the protected area (territory) and occasionally extended 100 or more yards from her nest site." From live trapping experiments, plotting the positions of capture of individuals on a map of the area covered, I interpreted (*op. cit.*, p. 28) the results to mean that there was territorial behavior in the white-footed mouse (*Peromyscus leucopus*), a nocturnal form. When the ranges of the various individuals were plotted on a map, I found that "the area of each of the breeding females is separate—that although areas sometimes adjoin one another, they seldom overlap." Carpenter (1942) writes thus: "The organized groups of every type of monkey or ape which has been adequately observed in its native habitat, have been found to possess territories and to defend these ranges from all other groups of the same species." In reporting on his work on the meadow vole (*Microtus pennsylvanicus*), Blair (1940, pp. 154–155) made the statement "It seems evident that there is some factor that tends to make the females occupy ranges that are in part exclusive; .... Possibly there is an antagonism between the females, particularly during the breeding season, but the available evidence does not indicate to me that they have definite territories which they defend against all trespassers. It seems highly probable that most mammalian females attempt to drive away intruders from the close vicinity of their nests containing young, *but this does not constitute territoriality in the sense that the term has been used* by Howard (1920), Nice (1937), and others *in reference to the breeding territories of birds.*" (Ital. mine.) To quote Howard (1920, pp. 192–193): "But the Guillemot is generally surrounded by other Guillemots, and the birds are often so densely packed along the ledges that there is scarcely standing room, so it seems, for all of them. Nevertheless the isolation of the individual is, in a sense, just as

complete as that of the individual Bunting, for each one is just as vigilant in resisting intrusion upon its few square feet as the Bunting is in guarding its many square yards, so that the evidence seems to show that that part of the inherited nature which is the basis of the territory is much the same in both species." Blair, in a later paper (1942, p. 31), writing of *Peromyscus maniculatus gracilis*, states: "The calculated home ranges of all sex and age classes broadly overlapped one another. Thus there was no occupation of exclusive home ranges by breeding females. . . . That individual woodland deer-mice are highly tolerant of one another is indicated by the foregoing discussion of overlapping home ranges of all sex and age classes." Reporting on an extensive field study of the opossum, Lay (1942, p. 149) states that "The ranges of individual opossums overlapped so frequently that no discernible tendency towards establishment of individual territories could be detected. On the contrary, tracks rarely showed that two or more opossums traveled together." It seems quite evident that both Blair and Lay are considering the home range as synonymous with the territory when in fact they are two quite distinct concepts. Further, there is no concrete evidence in either of the above papers for or against territoriality in the species they studied. It is to be expected that the territory of each and every individual will be trespassed sooner or later regardless of how vigilant the occupant of that territory might be.

It is not intended here to give a complete list of works on territorial behavior. The bibliographies in the works cited above lead to a great mass of literature on the subject. The point I wish to emphasize is that nearly all who have critically studied the behavior of wild mammals have found this behavioristic trait inherent in the species with which they worked. Also, it should be stressed, there are two fundamental types of territoriality in mammals—one concerns breeding and rearing of young, the other food and shelter. These two may be further subdivided to fit special cases. Mrs. Nice (1941) gives six major types of territories for birds. Our knowledge of territoriality in mammals is yet too limited, it seems to me, to build an elaborate classification of types. Some day we may catch up with the ornithologists.

HOME RANGE

The home range concept is, in my opinion, entirely different from, although associated with, the territoriality concept. The two terms have been used so loosely, as synonyms in many instances, that I propose to dwell briefly on them here. My latest Webster's dictionary (published in 1938), although satisfactory in most respects, does not list "home range," so I find no help there. Seton (1909) used the term extensively in his "Lives" where he explains it as follows: "No wild animal roams at random over the country: each has a home region, even if it has not an actual home. The size of this home region corresponds somewhat with the size of the animal. Flesh-eaters as a class have a larger home region than herb-eaters." I believe Seton was thinking of the adult animal when he wrote the above. We know that young adolescent animals often do a bit of wandering in search of a home region. During this time they do not have a home, nor, as I consider it, a home range. It is only after they

establish themselves, normally for the remainder of their lives, unless disturbed, that one can rightfully speak of the home range. Even then I would restrict the home range to that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range. The home range need not cover the same area during the life of the individual. Often animals will move from one area to another, thereby abandoning the old home range and setting up a new one. Migratory animals have different home ranges in summer and winter—the migratory route is not considered part of the home range of the animal. The size of the home range may vary with sex, possibly age, and season. Population density also may influence the size of the home range and cause it to coincide more closely with the size of the territory. Home ranges of different individuals may, and do, overlap. This area of overlap is neutral range and does not constitute part of the more restricted territory of animals possessing this attribute. Home ranges are rarely, if ever, in convenient geometric designs. Many home ranges probably are somewhat ameboid in outline, and to connect the outlying points gives a false impression of the actual area covered. Not only that, it may indicate a larger range than really exists. A calculated home range based on trapping records, therefore, is no more than a convenient index to size. Overlapping of home ranges, based on these calculated areas, thus may at times be exaggerated. From trapping records alone, territory may be indicated, if concentrations of points of capture segregate out, but it cannot be demonstrated without question. If the occupant of an area is in a trap, it is not in a position to defend that area. It is only by direct observation that one can be absolutely certain of territoriality.

Home range then is the area, usually around a home site, over which the animal normally travels in search of food. Territory is the protected part of the home range, be it the entire home range or only the nest. Every kind of mammal may be said to have a home range, stationary or shifting. Only those that protect some part of the home range, by fighting or agressive gestures, from others of their kind, during some phase of their lives, may be said to have territories.

SIGNIFICANCE OF BEHAVIORISTIC STUDIES

I think it will be evident that more critical studies in the behavior of wild animals are needed. We are now spending thousands of dollars each year in an attempt to manage some of our wild creatures, especially game species. How can we manage any species until we know its fundamental behavior pattern? What good is there in releasing a thousand animals in an area large enough to support but fifty? Each animal must have so much living room in addition to other essentials of life. The amount of living room may vary somewhat, but for a given species it probably is within certain definable limits. This has all been said before by eminent students of wildlife, but many of us learn only by repetition. May this serve to drive the point home once more.

ity. She was supposed to be five years of age when she was acquired by the San Diego Zoological Society.

The accessory nipple is a rudimentary one about one-half the diameter of the normal nipple. It is located 1.5 inches below the right nipple on the milk line, and 2.5 inches closer to the midline than the normal nipple above it. Records of polymastia and polythelia are frequent in man, but the asymmetrical outnumber the symmetrical ones, with the left side most often affected. In this Journal (February 1933, p. 66) I recorded the first case of symmetrical supernumerary mammae in a chimpanzee. In view of the fact that accessory nipples

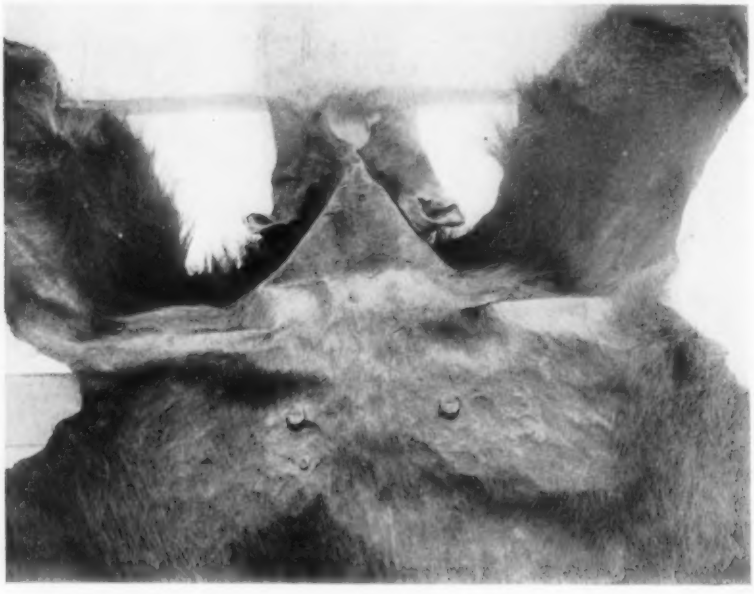

PLATE 2

Accessory nipple in a chimpanzee

appear in probably one percent of human cases, in the siamang and gibbon this anomaly might easily be overlooked on account of the thickly haired hide, unless the nipple were fairly well developed in a captive animal, such as the one here described. I recently learned that "Blackie" died during the summer of 1941.

I am also able to record the case of a supernumerary nipple in a gibbon. My friend and colleague on the Asiatic Primate Expedition (1937), Dr. Adolph H. Schultz, found the first case of an extra nipple in a female *Hylobates lar* No. 158 A.S. I am grateful to him for letting me publish it. He also found a considerable number of other congenital malformations in the gibbon series collected by the expedition at Doi Angka, N. Thailand. His field notes read: "left nipple

has accessory nipple, lateral to larger normal one; this animal has medium size nipples and small mammary glands." Examination of the specimen shows that the accessory nipple after being fixed in 10 percent formalin is 2 mm to the left side of the base of the left nipple emanating from the actual basal tissue, making a sort of double nipple (fig. 1). The basal diameter of the accessory is 3 mm with a length of 8 mm, as compared with a base of 14.5 mm x 13 mm and a length of 25 mm in the normal nipple. Through the courtesy of Dr. George Wislocki, the accessory nipple was sectioned.

The sections reveal a slender, nipple-like structure about 8 mm long and 1½ to 2 mm in diameter. The structure consists of a central core of connective tissue, covered by epidermis, and continuous at its base with the corium and epidermis of the neighboring skin. The epidermis covering it is pigmented in its deepest layer, and the epidermis projects at the tip and sides more irregularly into the corium than in the surrounding skin. The structure possesses neither hairs nor sebaceous or sweat glands, although these are visible in the skin ad-

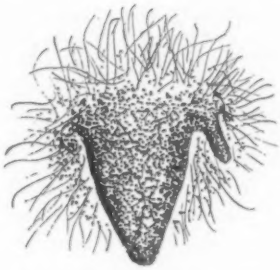

FIG. 1. Accessory nipple in a gibbon

jacent to the base. No duct or system of ducts can be seen in the interior of the appendage. The central core of connective tissue appears to be supplied with an excessive blood supply consisting of small, branching arteries and capillaries. Small bundles of nerves can be traced into the central core. These last two observations suggest that the appendage in question may be erectile. Beneath the structure, in the neighboring and subjacent subcutaneous tissue, mammary gland tissue and ducts are plentiful, but these ducts are not directly related to, and do not traverse, the appendage under consideration.

In the collection of the late Major Powell-Cotton, there is a fully adult female chimpanzee specimen (no. M 670) that was collected in the Batouri district of the Cameroons by F. G. Murfield in October 1933. The skin of this animal shows an accessory nipple on the milk line somewhat below the normal right nipple. I am grateful to Mr. G. F. Pinfold of the Powell-Cotton Museum for sending me this information.

It is hoped that when further cases of supernumerary mammae or nipples are discovered by taxonomists that they will be reported so that we can better

compare this anomaly, particularly in the anthropoid apes, with similar cases that are so well known in man.

An interesting recent paper on the supernumerary breast was published (Arch. of Surg., vol. 39, pp. 936–941. 1941) by Dr. Tibor de Cholnoky in which he describes a pseudo mamma in a human male and an unusually complete breast in a female, both of them located on the inner aspect of the right thigh.

Dr. Harold Speert has recently published (Quart. Rev. Biol., vol. 17, no. 1, pp. 59–68. 1942) an excellent article on supernumerary mammae, with special reference to the rhesus monkey, in which he draws attention to the paucity of information on this subject in sub-human primates.

Museum of Comparative Zoology, Cambridge, Massachusetts.

MIOCENE BAT REMAINS FROM FLORIDA, WITH NOTES ON THE GENERIC CHARACTERS OF THE HUMERUS OF BATS

By Barbara Lawrence

Among the many interesting finds made by Dr. Theodore E. White at the Thomas Farm site near Gainesville, Florida, are three humeri of primitive vespertilionid bats and parts of two lower jaws, probably not related to the long bones. The material is fragmentary, but the rarity of fossil bat remains from North America has made it seem worthwhile to study them in detail. The jaws are without teeth and their positive identification is difficult. The humeri, one complete, one slightly broken at the proximal end, and one distal half, represent two undescribed genera, one considerably more primitive than the other. The value of this material depends entirely on the extent to which the humerus is characteristic of different genera of bats. Since little has been done in this field considerable research was necessary before any comparisons of this fossil material were possible. One of the results of this work was the discovery that the humerus in bats is of far greater taxonomic importance than was previously supposed. This is not surprising in a flying mammal where any small changes in the mechanism of flight would have immediate bearing on the life habits of the animal. Small differences in the skin and skull are, as is well understood, useful for telling species and races apart; for grouping species in genera and understanding the larger relationships, the characters of the humerus and probably also those of the rest of the forelimb and shoulder girdle are of great importance.

Individuals from the principal North American genera were studied to determine the differences between genera, and five species of *Myotis* were studied to determine the amount of variation that might be expected within the genus. *Myotis* was selected for this more detailed study as it is the genus most closely related to the two new fossil forms. Specimens examined include *Antrozous pallidus, Corynorhinus rafinesquii pallescens, Eptesicus fuscus, Nycticeius humeralis, Lasionycteris noctivagans, Pipistrellus subflavus, Lasiurus borealis, Dasypt-*

erus floridanus, *Nyctalus noctula*, *Miniopterus schreibersii blepotis*, *Myotis myotis*, *M. lucifugus*, *M. austroriparius*, and twelve specimens each of *M. grisescens* and *M. velifer incautus*.

The structure of the shoulder girdle and wing bones in bats has been well described by Miller (1907, p. 12–20), and the characters distinguishing the humeri of the various families given in some detail together with an account of their evolutionary significance. He points out that the Vespertilionidae, in particular, are characterized by the proportionally great development of the trochiter, distal articular surface not displaced outward, and the small epitrochlea supporting a high spinous process. In the course of preparing this paper it has become apparent that, within certain broad limits, there is considerable *generic* variation in all of the above characters. Revilliod (1920, pp. 95–96), although not basing his descriptions of fossil forms on humeri alone, still recognizes their importance, and in a comparison of *Taphozous* and the related fossil genus *Vespertiliavus* gives as important differences the shape and angle of the head of the humerus (*i.e.* whether the main axis is vertical or inclined inwards), the position and size of the fossae for the insertion of the sub- and supra-spinous muscles, the relation of width of distal extremity to length of shaft, depth of olecranon fossa, structure of the external condyle and size of the styloid (spinous) process of the epitrochlea. In the same paper, (p. 116–117), he compares the humeri of two Molossidae of different genera, *Molossus obscurus* and *Nyctinomus stehlini*. In these he considers the less lengthened head of the humerus, broad tuberculum minus (trochin), larger trochlea, and shorter styloid (spinous) process as differential and more primitive characters of the latter. As regards the Vespertilionidae, most of Revilliod's characters are equally diagnostic of genera, except perhaps the development of the spinous process of the epitrochlea; this, in *Myotis* at least, varies markedly within the genus. The position of the fossae for the insertion of the sub- and supra-spinous muscles varies the least from one genus to the next.

RECENT HUMERI

In general, humeri of *Myotis* (fig. I, A–D) may be distinguished from those of the other Vespertilionidae by the slender shaft with a minimum dorsal width of less than 50 percent that of the epiphyses and the nearly equal width of the epiphyses. In the species examined the dorsal width of the shaft is between 36 and 43 percent that of the distal epiphysis and between 33 and 39 percent that of the proximal; the width of the distal epiphysis is between 89 and 97 percent that of the proximal.

Viewed from in front, the whole upper end of the shaft is tilted slightly inward, while in profile the shaft is nearly straight in some species, as *austroriparius* and *lucifugus*, and slightly concave backwards in others. The head is relatively large, oval to nearly round, with a slight flattening of the outer upper side. The trochiter, as compared with that of other members of the family, is low in relation to the head, and the lateral ridge from the trochin extends for three-quarters the length of the deltoid crest (see fig. 1, A5). Distally, the proportional de-

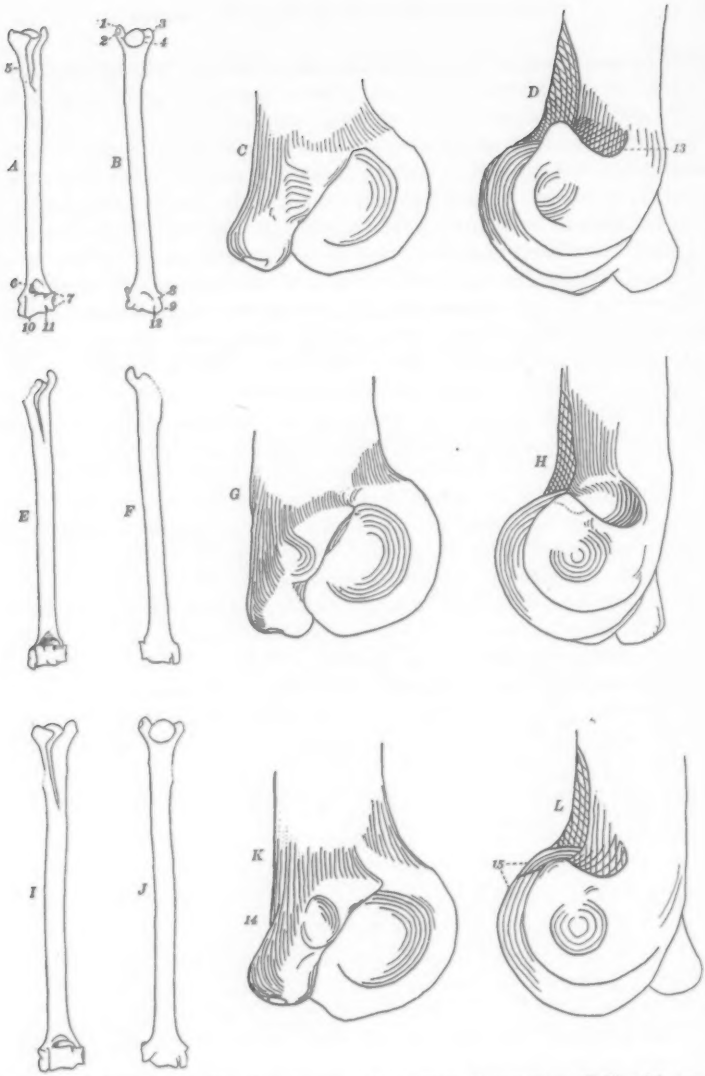

FIG. 1. Left humerus in *Myotis grisescens*: A anterior, B posterior, C distal internal, D distal external views; E, F, G, H, the same in *Miomyotis floridanus*, (E, F, H, type; G, holotype); I, J, K, L, the same in type of *Suaptenos whitei*.

For all figures: 1, trochiter; 2, fossa for insertion of subspinous muscle; 3, trochin; 4, head; 5, lateral ridge from trochin; 6, radial fossa; 7, ridge of capitellum; 8, epitrochlea; 9, spinous process of epitrochlea; 10, trochlea; 11, capitellum; 12, groove separating trochlea from spinous process; 13, reentrant proximal to ridge of capitellum; 14, median fossa of epitrochlea; 15, rounded portion of capitellum; 16, olecranon fossa. Length ×2; distal extremity ×15.

velopment of capitellum and trochlea, shallow radial fossa, olecranon fossa reduced to a faint depression, great development of the epitrochlea supporting a blunt styloid process which is separated from the trochlea by a distinct but shallow groove, slight backward tilt of the combined epitrochlea and spinous process when seen from the side, and deep reentrant proximal to the ridge of the capitellum (fig. 1, D13) are all conspicuous features of the genus. The grooves and ridges of the articular surface are shallow and low and roughly parallel to the main axis of the shaft. Specific variation is found in the amount of antero-posterior curvature of the shaft, width of the epitrochlea and size of the styloid process, amount of lateral displacement of the distal articular surface, details of points for insertion of muscles on epitrochlea and styloid process, and shape of trochiter and fossae for insertion of sub- and supra-spinous muscles.

Among the other North American genera, variation from the *Myotis*-like humerus is in two directions. On the one extreme is the less specialized type found in *Antrozous*, (fig. 2, A–D), on the other, the highly specialized type found in *Lasiurus*, (fig. 2, E–H). *Antrozous* has a narrow shaft and broad, equally developed epiphyses (width of shaft about 37 percent that of both proximal and distal epiphyses); viewed anteriorly, the shaft has a slight S-curve; from the side the distal curvature of the shaft is more pronounced than in *Myotis* and is somewhat compensated for by a slight reverse curve proximally. The trochiter is low; small head, round; combined capitellum and trochlea, relatively narrow; the broad epitrochlea supports no spinous process; olecranon fossa, absent; radial fossa, extremely shallow. *Corynorhinus* is in many ways similar to this, only less extreme. The shaft is broader in comparison to the epiphyses (width of shaft about 47 percent that of distal epiphysis and 40 percent that of proximal), and the distal epiphysis is slightly narrower in relation to the proximal than in *Myotis* (about 86 percent that of the proximal). The curvature of the shaft as seen from the front is greater than in *Antrozous*; from the side, less. However, this character is specifically variable within certain limits. The trochiter is low, and the shape and relative size of the head about as in *Myotis*, as is the faint suggestion of an olecranon fossa; the very shallow radial fossa is more like that of *Antrozous*. The epitrochlea is only slightly narrower in proportion to the articular surface than in *Antrozous* and supports no spinous process. In both genera the ridges and grooves of the articular surface are in general *Myotis*-like.

Eptesicus, although it resembles *Antrozous* and *Corynorhinus* in its low trochiter and lack of a spinous process, is no closer to these two than it is to *Myotis*. In the small size of the head it resembles *Antrozous*, in proportional width of shaft and epiphyses, *Corynorhinus*. The radial fossa, however, is larger than in either; the epitrochlea proportionally, smaller. *Nycticeius* is not significantly different from *Eptesicus* in outline and proportion of distal to proximal epiphyses; the shaft itself is slightly narrower in relation to the epiphyses. In shape of head and height of trochiter the two are very close. Distally the epiphysis resembles in many ways that of *Lasionycteris*, for the small epitrochlea, the

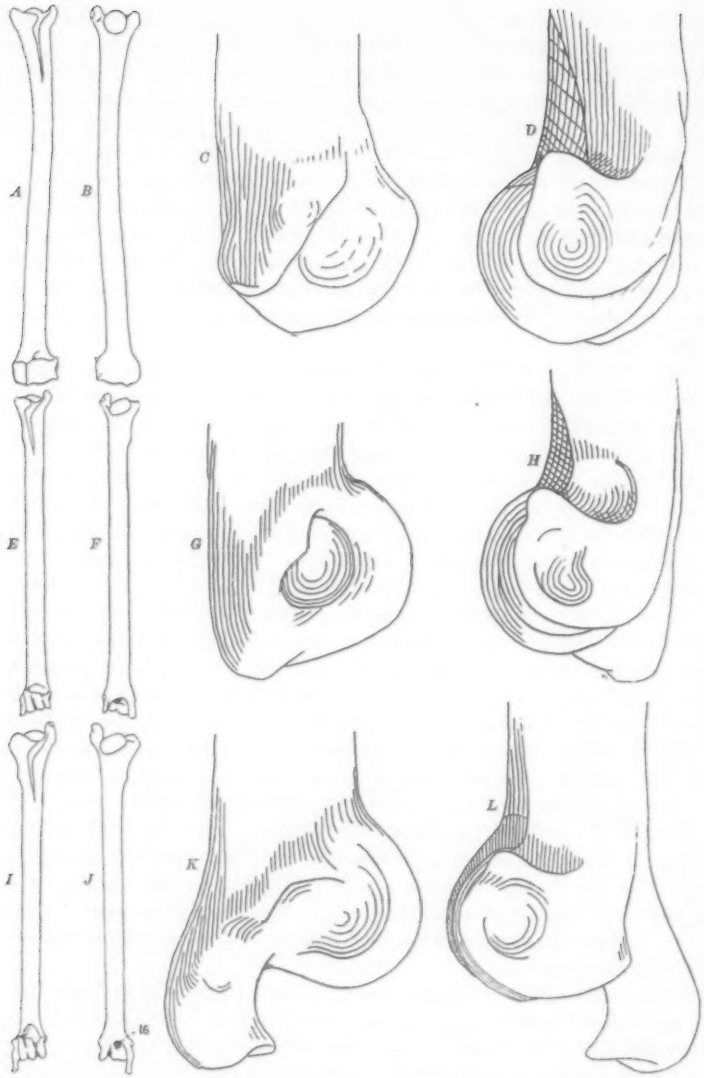

FIG. 2. Left humerus in *Antrozous pallidus*: A anterior, B posterior, C distal internal, D distal external views; E, F, G, H, the same in *Lasiurus borealis*; I, J, K, L, the same in *Miniopterus schreibersii blepotis*. Numbers and enlargements as in fig. 1.

posterior development of this and the low spinous process, as well as the deeper radial fossa, suggest this genus.

In *Lasionycteris* we have a slight development of a type that finds its extreme in *Lasiurus*. In the former, the distal epiphysis is narrower in relation to the proximal; the trochiter higher in relation to the head than in *Myotis*; the head itself more oval than round and tilted inwards; the lower internal side slightly flattened and the upper external side markedly so; the groove separating trochin and head shallower than in *Myotis*; the shaft even more curved, both from front and side views, than in the latter. Distally, the articular surface is wide, the proportionally small epitrochlea supports a low spinous process, which is situated more posteriorly than laterally. This shifting in position of the spinous process is associated with an antero-posterior expansion of the epitrochlea, which forms a raised margin along the inner side of the olecranon fossa and is continued along its superior border as a low ridge. The grooves of the trochlea and capitellum are somewhat deeper than in *Myotis*, although roughly parallel to the main axis of the shaft. *Pipistrellus* represents another stage in the development of this type of humerus, the proximal epiphysis is even larger in relation to the distal, with a high trochiter and a small elongated head flattened on the upper external and lower internal side. When seen from the anterior side the small epitrochlea scarcely projects beyond the trochlea; there is a small knob-like spinous process. The whole distal articular surface has shifted forward without an accompanying curvature of the shaft so that posteriorly, on the internal upper border of the olecranon fossa, a deep pocket is formed, which receives the sharpened edge of the combined radius and ulna. There is no tilting back of the spinous process, the posterior margin being in line with the shaft. The radial fossa is deep. Internally the trochlea has a broad, flat ridge much greater in diameter than the ridge of the capitellum, and the deep trochlear groove is at an angle to the main axis of the shaft.

Lasiurus represents an extreme development of this type of humerus and in this respect resembles the Old World genus *Nyctalus*. Both have a straight, thick shaft, broad in comparison to the distal epiphysis (in *Nyctalus* width of shaft is about 56 percent that of the distal epiphysis; in *Lasiurus*, about 62 percent), and the proximal epiphysis is much wider in comparison to the distal (in *Nyctalus* the width of the distal epiphysis is about 63 percent that of the proximal; in *Lasiurus*, about 62 percent). The trochiter is almost as high in relation to trochin and head as in the Molossidae; the head is oval and flattened, inclined inward with a connecting ridge rather than a groove between its upper, internal end and the trochin. Distally, the broad articular surface and development of a pocket-like olecranon fossa to receive the edge of radius and ulna, apparent in both genera, are most extreme in *Lasiurus*.

Miniopterus (fig. 2, I–L) is quite unlike any other vespertilionid genus examined, and is in many ways intermediate between this family and the Molossidae. The pocket-like development distally of the olecranon fossa (see fig. 2, J16) is similar to that in *Lasiurus*, only much more extreme, and is distinct in that

TABLE 1—*Comparisons of lower jaws in fossil and Recent bats*

	EPTESICUS FUSCUS OSCEOLA	LARGE FOSSIL M.C.Z. 4057	SMALL FOSSIL M.C.Z. 4058	NYCTICEIUS HUMERALIS
Sockets of incisors	Socket for I_1 largest. I_3 somewhat crowded forward, I_2 flattened anteriorly.	Sockets for I_1 & I_2 equal in size and rounded; smaller socket for I_2 flattened between them.	Missing.	Sockets subequal in size, round, I_3 not markedly crowded out of line.
Socket for Pm_3	About same size as socket for anterior root of Pm_4.	Larger than socket for either root of Pm_4.	As in large fossil.	Slightly smaller than socket for either root of Pm_4.
	Not flattened antero-posteriorly and scarcely broader than long.	Flattened antero-posteriorly and markedly broader than long.	As in large fossil.	Round.
Sockets for Pm_4	Anterior socket slightly smaller than posterior.	Sockets same size.	As in large fossil.	About as in *E. f. osceola*
	Rounded.	More flattened and compressed.	As in large fossil.	Anterior slightly flattened.
Sockets of M_1	Socket for anterior root of M_1 somewhat larger than that for posterior root of Pm_4	Socket for anterior root of M_1 conspicuously larger than that for posterior root of Pm_4.	As in large fossil.	Socket for anterior root of M_1 not conspicuously larger than that for posterior root of Pm_4.
Shape of anterior part of jaw	Jaw not abruptly narrowed anterior to canine. No ridge.	Jaw anterior to canine not abruptly narrowed, twice as wide as socket for I_3 and having a ridge that	Missing	Jaw abruptly narrowed anterior to canine.

TABLE 1—*Concluded*

	EPTESICUS FUSCUS OSCEOLA	LARGE FOSSIL M.C.Z. 4057	SMALL FOSSIL M.C.Z. 4058	NYCTICEIUS HUMERALIS
Shape of anterior part of jaw—*cont.*		runs from the inner margin of the alveolus of C to the inner margin of the alveolus of I_1.		
Symphysis of jaw	Symphysis of jaw curving back to a ventral projection below posterior margin of alveolus of Pm_3.	Symphysis of jaw curving back to a ventral projection below anterior margin of alveolus of Pm_3.	Anterior part of jaw broken but ventral projection shows below alveolus of Pm_3.	Symphysis of jaw more vertical, greatest ventral projection below alveolus of C.
Mental foramen	Diameter equals length of alveolus of Pm_3; situated below sockets for Pm_3 and for anterior root of Pm_4, midway between alveolar margin and bottom of jaw.	Diameter less than length of alveolus of Pm_3; situated below posterior edge of C one-third of distance from alveolar margin to bottom of jaw.	Diameter conspicuously greater than length of alveolus of Pm_3; situated below alveolus of Pm_3 and midway from alveolar margin to bottom of jaw.	Diameter equals length of alveolus of Pm_3; situated slightly anterior to alveolus of Pm_3 and about midway from alveolar margin to bottom of jaw.
Alveolar height of jaw immediately posterior to Pm_4.	2.5	2.0	2.0	1.7
Thickness of jaw immediately posterior to Pm_4.	1.1	.9	.8	.7

it receives the sharpened edge of the ulna only. The long low deltoid crest is characteristic of the Vespertilionidae. The extremely long curving spinous process, deep trochlear groove, deep radial fossa, and narrow epitrochlea are characteristic of the Molossidae; the first two features are even more extreme than in any other molossid genus examined.

FOSSIL HUMERI

Of the two new Miocene genera, the larger and apparently more primitive may be known as:

Suaptenos, gen. nov.

Diagnosis.—Humerus with trochiter slightly higher than head, about equal in breadth to trochin, and having a third fossa above that for the insertion of the subspinous muscle and posterior to that for the insertion of the supraspinous muscle; distal articular surface displaced laterally so that a vertical from the edge of the trochlea falls on the narrow portion of the shaft instead of external to it; epitrochlea well developed, supporting a blunt spinous process separated from the trochlea by a distinct groove; posterior margin of combined epitrochlea and spinous process tilted back forming an obtuse angle with main axis of shaft; ridge of capitellum small, projection of upper margin low, when seen in profile, not as high as rounded portion of capitellum in front of radial fossa (see fig. 1, L15), depth of reentrant on outer side immediately proximal to ridge less than half thickness of shaft at this point.

Comparisons—*Suaptenos*, when compared with *Myotis*, has the relation of width of distal extremities to each other and to width of shaft almost as in the latter, with the proximal epiphysis relatively a little narrower than in the Recent genus. Seen from in front, the proximal end appears less tilted, although, owing to a break in the shaft, it is difficult to establish this point conclusively; in side view, there is more curvature of the shaft in the fossil form. The larger head is similar in shape to that of *Myotis*, but both trochiter and trochin are relatively low and the groove separating the latter from the head is shallow. Distally, the articular surface is more displaced laterally than in any *Myotis* examined; the epitrochlea, broader; the distinct, though short and truncated, spinous process, entirely lateral, separated from the trochlea by a well marked groove. Of the various genera examined, this groove is found only in *Myotis* and is better developed in some species than in others, although, owing to the posterolateral position of the reduced spinous process, it never extends up the dorsal side of the shaft as it does in *Suaptenos*, in which it extends for about two thirds the height of the epitrochlea. In the latter, the combined epitrochlea and spinous process tilt back away from the main axis of the shaft as in *Myotis* and the grooves and ridges of the articular surface are parallel to this axis. In reduction of the olecranon fossa, *Suaptenos* resembles *Myotis*, but the radial fossa is peculiar in having a median transverse ridge separating a low, broad, relatively deep distal portion from a much shallower proximal one. The latter appears to be more closely connected with the trochlear margin and it is possible

that this is the remnant of the ulnar fossa which in Recent forms, with the exception of *Lasionycteris*, is entirely merged with the radial.

Suaptenos whitei, sp. nov.

Type.—Humerus, M. C. Z. no. 4056; Lower Miocene, Hawthorne formation; Thomas Farm, 15 miles west of High Springs, Gilchrist County, Florida; collected by Theodore E. White, 1942.

Diagnosis.—*Suaptenos whitei* may be distinguished by its large size (length of humerus 29.1 mm); curving shaft as seen in side view; proportionally broad epitrochlea (about 30 percent of total width of distal epiphysis); broad blunt spinous process not extending below capitellum, groove between it and trochlea moderate; deep median fossa on the epitrochlea, (see fig. 1, K14) bounded posteriorly by a sharpened margin. The trochiter is elongated anteroposteriorly with basal portion not constricted and with only a slight concavity where it merges with the outer edge of the deltoid crest; fossa for insertion of the subspinous muscle exceptionally deep with a sharp projection at its antero-inferior edge.

The smaller Miocene genus may be known as:

Miomyotis, gen. nov.

Diagnosis.—Humerus with distal articular surface not displaced laterally, vertical from edge of trochlea falls external to shaft; epitrochlea moderately developed, supporting a blunt spinous process, separated from trochlea by a groove, with a sharpened inner edge overhanging the groove; posterior margin of combined epitrochlea and spinous process in line with main axis of shaft; ridge of capitellum as in *Suaptenos*, depth of reentrant proximal to this greater than half the thickness of shaft at this point; trochlear groove and ridge of capitellum not parallel with main axis of shaft.

Comparisons.—Compared with *Suaptenos*, *Miomyotis* differs chiefly in the proportionally broader articular surface and narrower epitrochlea. The actual shape of the spinous process, somewhat curving forward and overhanging the groove separating it from the trochlea and forming a raised, sharpened margin as seen from in back is quite distinctive. The shaft is straighter in *Miomyotis*, both in front and side views, the radial fossa deeper and broader. The head of the shaft is unfortunately somewhat broken, but the trochiter appears to be narrower than in *Suaptenos* and the ridge from the trochiter long, as in *Myotis*. In smaller size of the epitrochlea and position of the distal articular surface in relation to the shaft, it resembles *Myotis* more closely than does *Suaptenos*.

Miomyotis floridanus, sp. nov.

Type.—Humerus, M. C. Z. no. 4055; Lower Miocene, Hawthorne formation; Thomas Farm, 15 miles west of High Springs, Gilchrist County, Florida; collected by Theodore E. White, 1942.

Diagnosis.—*Miomyotis floridanus* may be distinguished by its medium size (length of humerus 24.8 mm); shaft nearly straight as seen in side view; epi-

trochlea narrow (about 20 percent of total width of distal epiphysis); small spinous process extending below as far as capitellum, groove between it and trochlea deep; shallow fossa on epitrochlea with upper posterior margin not sharpened but merging gradually with back of shaft. Trochlear groove and ridge of capitellum at a slight angle to main axis of shaft.

DISCUSSION

The discovery in the early Miocene of Florida of representatives of the *Myotis* group of the Vespertilonidae is not surprising. *Myotis* as a genus is well represented as early as the middle Oligocene in Europe and various allied genera have been described from even earlier formations. Chief among these, and coming from the Quercy deposits of the late Eocene and early Oligocene, is Revilliod's *Nycterobius gracilis* (1922, pp. 133–136), based on cranial fragments and said to be not unlike *Myotis*. Of the various vespertilionid species mentioned by Revilliod (*op. cit.*, p. 179), but not assigned to genera, all are very fragmentary and none include humeri. Two humeri from Quercy not identified even as far as family are also figured (*op. cit.*, p. 155, figs. 61, 62) and bear little resemblance to the Florida material. Humerus "a" is described (*op. cit.*, p. 154–156) as resembling most closely *Miniopterus*, although he felt the material not sufficient actually to include it in this genus. Humerus "b" (*op. cit.*, p. p. 156) has the proximal end broken, only a short section of the deltoid crest remaining. The distal end is said to be similar in general to that of *Myotis*, although the greater development of the epitrochlea is reminiscent of *Vespertiliavus* from Quercy. From the figure given, it appears that this humerus is not as close to *Myotis* as was originally believed. The width of the epitrochlea, the deep valley separating it from the trochlea, the rounded capitellum, and proportionally small articular surface markedly displaced laterally, as well as the broken stub of a well-developed spinous process are all quite different not only from *Myotis* but also from other Vespertilionidae examined. The distal portion of a small humerus from the Oligocene of Frankfurt a. M. is also figured (*op. cit.*, p. 157, fig. 63) and described as being reminiscent of *Miniopterus*, although the figure does not make this resemblance entirely clear. That a typical *Myotis* humerus was developed as early as the late Oligocene in Europe is shown by the fragment of a distal end figured by Schlosser (1887, pl. 2, fig. 43) as *Vespertilio insignis* and quite properly assigned by Revilliod (1922, p. 166) to the genus *Myotis*. Thus the evidence is that at this early date *Myotis* had assumed its characteristic form, and the genera *Suaptenos* and *Miomyotis* should be considered, not as ancestral to *Myotis*, but as allied, more primitive genera, which have not survived to the present.

From North America the scanty records of Tertiary bats include no previous mention of any *Myotis*-like genera, nor, with the exception of Jepsen's as yet undescribed Green River Eocene skeleton, any conclusive evidence of bat remains from as early as the Lower Miocene. Matthew (1917, p. 569), reviewing the status of Marsh's genera *Nyctitherium* and *Nyctilestes* and of Cope's *Vesperugo*, summarizes thus: "In North America no conclusive evidence of Tertiary

bats has hitherto been recorded." He then describes *Zanycteris paleocenus* from the Upper Paleocene or lowest Eocene as the earliest chiropteran on record. In a later discussion of the type, G. M. Allen (1939, pp. 176–177) indicates that the specimen, almost certainly not a bat, is probably an insectivore. Two more recently described vespertilionid genera are interesting in that they belong to groups, which, from the European record, appear to be old. *Mystipterus vespertilio* Hall (1930, p. 319), from the Lower Pliocene or Upper Miocene of Fish Lake Valley, Esmeralda Co., Nevada, is based on a lower jaw fragment with the last molar in place, and most closely resembles the Recent genus *Miniopterus*, although the author is careful to point out that such evidence is not sufficient to establish a "near genetic relationship." *Simonycteris stocki*, referred to below, is a relative of *Eptesicus*. Study of these Florida humeri corroborates in an interesting way Revilliod's and Miller's statements as to the primitive nature of the genus *Myotis*. That the genus is geologically old has already been amply demonstrated by the number of species found in European deposits beginning with those from the middle Oligocene. Discovery of these two related genera with such characters as a low trochiter, rounded head, proportionally broad distal epiphysis, and broad epitrochlea lend further credence to the theory that this type of humerus is a primitive one, as do the various observable stages of development, starting from a *Myotis*-like humerus and culminating in the *Lasiurus* type with its highly specialized locking mechanism in the elbow joint. Just what bearing this mechanism has on the method of flight is yet to be worked out. It appears clear, however, that it eliminates almost entirely any such rotation of this joint as is found in birds, giving it instead a hinge action and, on the down stroke, considerable rigidity. That it is found in the narrow-winged strong-flying bats, some of which are known to migrate long distances, seems to indicate that this type of humerus is a specialization of the more primitive one directly related to increased flying ability. If such is the case, the early appearance of the highly specialized sub-family Miniopterinae is most interesting.

FOSSIL JAWS

Associated with the humeri, but probably generically different, are fragments of the anterior parts of two lower jaws without teeth. The larger is complete from the posterior socket of M_2 to the mental symphysis, the smaller from the anterior socket of M_2 to the canine. The alveoli are in good condition, the smaller jaw even includes the roots of Pm_4, and it is possible to determine that both individuals had two premolars, the second one double rooted. Of the various vespertilionid bats with this tooth formula, the fragments at hand most closely resemble *Eptesicus fuscus* in massiveness, relative size of the alveoli, and shape of the jaw anterior to the canine; in length of tooth row they are close to *Nycticeius humeralis*.

Both fossil jaws are smaller than in the Recent Florida form, *Eptesicus fuscus osceola*, and the even larger Pleistocene *E. f. grandis*; the apparent lack of reduction of Pm_3 as well as the more even size and spacing of the alveoli of the

incisors indicates a somewhat more primitive form, although any specific or generic diagnosis based on such fragmentary material would be entirely inadequate. An *Eptesicus*-like bat from the Pliocene, *Simonycteris stocki*, was described by Stirton (1931, pp. 27–30) from the San Pedro formation of Arizona. The name is based on a fragment of palate and rostrum and the genus is distinguished from *Eptesicus* chiefly by its abrupt facial angle and shortened rostrum. The compressed flattened sockets in the Florida specimens suggest just such a shortening of the jaws as one would expect to find in *Simonycteris*, and it is possible that the Florida forms may be related to this genus. From Europe, the much discussed *Vespertilio murinoides* Lartet (see Revilliod, 1922, pp. 167–168) from the Vindobonian Miocene was based on lower jaw fragments without teeth. The tooth formula apparently is the same as that of *Eptesicus* and the Florida jaws. The figures of this material in Gervais (1848–52, pl. 44, figs. 5–7) show the sockets for the premolars are less compressed and more rounded than in the Florida fossils, resembling *Eptesicus* in this respect. There is also a definite space between the canines and the incisors, and the latter are not crowded. Particularly in the specimen figured as 7 and 7a, the jaw anterior to the canine appears elongated and the widely spaced sockets for the incisors are subequal in size, differing in this from both *Eptesicus* and the Florida fossil jaws. In the high anterior position of the small mental foramen there is a marked resemblance to the large Florida specimen. The genus *Samonycteris* from the late Miocene (Revilliod, *op. cit.*, pp. 139–144) is described from a skull with the lower jaw in place as "un genre voisin de notre Sérotine, mais dont l'évolution a été plus rapide. . .". Unfortunately the condition of the specimen was such that the jaw could not be detached and studied.

Thus it appears that *Eptesicus*-like bats had already made their appearance in the Middle Miocene in Europe. The Thomas Farm material, although admittedly very fragmentary, still is identifiable as related to *Eptesicus* and is important chiefly because it indicates the presence of an *Eptesicus*-like bat as far back as the Lower Miocene in North America.

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A NEW GENUS OF RODENTS FROM PERU

BY WILFRED H. OSGOOD

During two expeditions in recent years, Mr. Colin C. Sanborn spent considerable time in the highlands of Peru south and west of Lake Titicaca. His collections include most, if not all, of the small rodents that mark this region with nearby adjoining areas as having a high degree of endemism. Among them is a single specimen of a short-tailed and dull-colored mouse of such peculiarity that its generic distinction seems imperative. It may be characterized as follows:

Punomys lemminus new genus and species

Type.—Adult female; No. 49710, Field Museum of Natural History; from San Antonio de Esquilache, Department of Puno, Peru; altitude 15,000 feet; collected Sept. 21, 1939, by Colin C. Sanborn, original number 2191.

Generic and specific characteris.—A stoutly built mouse of medium size, short tail, relatively small ears, very long, soft, and loose pelage; coloration dull but upper parts sharply demarked from under parts; hind feet hairy only for their proximal fourth; pads and proportions of toes normal; claws uniformly small. Skull rather heavy with a heavy rostrum and well-developed nasals rather abruptly expanded anteriorly; dorsal outline slightly and evenly arched; braincase somewhat squared behind; interparietal strap-shaped, of moderate size; supraorbital edges with slight ridges continuing over parietals to supraoccipital and with slight expansions at the fronto-parietal suture suggesting incipient postorbital processes; zygomata rather light and slightly compressed anteriorly; "zygomatic plate" fairly wide, its front edge slightly convex and very slightly sloping backward, although definitely visible from above; palate with a narrow central ridge separating deep channels running from the anterior palatine foramina practically to the parapterygoid fossae from which they are separated only by a slight elevation behind two rounded pits situated one on each side of the rounded interpterygoid notch; pterygoid region and audital bullae not peculiar, the latter moderately inflated. *Dentition highly peculiar.* Upper incisors rather stout and heavy, not thrown forward, their front surfaces smooth; lower incisors separated by a considerable space. Upper maxillary teeth only moderately hypsodont, their grinding surfaces offering an apparent complexity due to the presence of styles and conules between all the principal elements in each tooth not only on the labial side but also on the lingual. Anterior tooth with six major elements and five minor ones; on the labial side, these are the parastyle, secondary parastyle, paracone, mesostyle, metacone, and metastyle, the last only slightly developed; on the lingual side are the protoconule, secondary protoconule, protocone, mesoconule, hypocone, and metaconule. The middle tooth similarly has four major elements and five minor elements. The last molar is slightly more than half the size

of the middle one but has four major elements and three minor ones. Lower grinding teeth correspondingly complex, the anterior one with six main and four minor divisions. Grinding surfaces of cheekteeth not flat, but worn principally in the middle line forming a trough between the primary cusps.

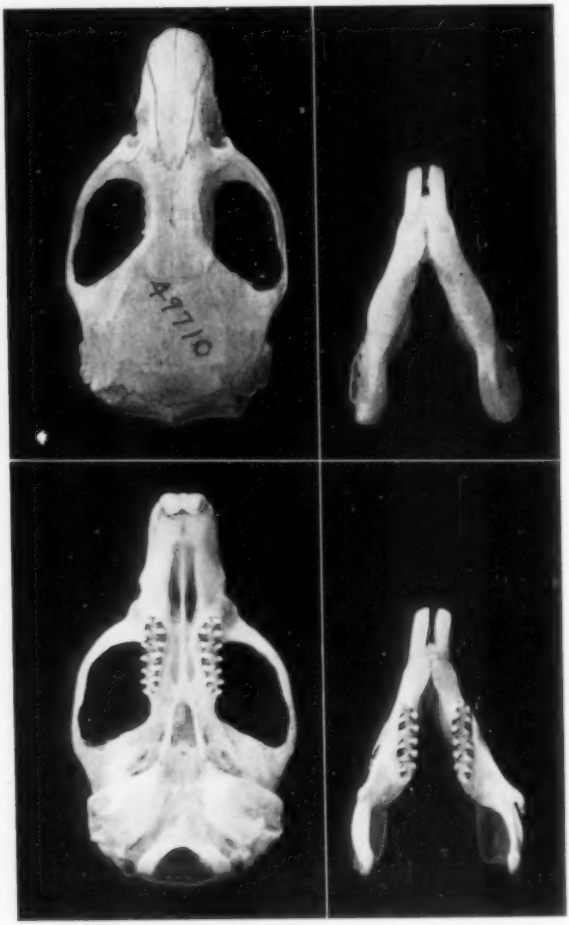

PLATE 1

Skull of type of Punomys lemminus

Color.—Upper parts and sides Buffy Brown lightly and uniformly mixed with dusky; no evident lateral line and no markings about head and face; ears hairy within and without, colored like surrounding parts except for a few whitish hairs on the inside; under parts uniform dull white, the plumbeous color, which occupies the basal three-fourths of the hairs,

showing through somewhat. Feet white; tail sharply bicolor, narrowly dusky above and white below.

Measurements.—Total length 185; tail 46; hind foot 29; ear from notch (dry) 16.5. Skull: greatest length 32.4; basal length 31.2; zygomatic breadth 17.5; breadth of braincase 14.8; interorbital constriction 4.1; median length of nasals 12.5; greatest breadth of nasals 4.7; width of zygomatic plate 3.8; diastema 7.4; palatal slits 6; maxillary toothrow (crowns) 6.5.

Remarks.—When the single specimen of this very extraordinary mouse was received, its peculiarities were noted but on account of its short tail and its high Andean habitat it was thought that it might be allied to *Galenomys garleppi*, another rare Andean species then known only from the type which is in the British Museum. Recently, however, Field Museum has received an excellent specimen of *Galenomys garleppi* collected by Francisco Steinbach at the type locality on Mount Sahama, Bolivia. This proves to be wholly different from *Punomys* and clearly allied to *Phyllotis* or *Auliscomys*. Externally it resembles *Phyllotis* in its large leafy ears and silky pelage and its dentition is not peculiar. Its hairy feet, very short tail and its arched skull with slightly proodont incisors may entitle it to generic or subgeneric recognition, but its affinity to *Phyllotis* and *Auliscomys* is obvious.

The pelage in *Punomys* is without much glossiness and is very long, very soft and, although dense, is still rather loose. Hairs on the back are about 18 millimeters in length. Aside from their other characters, the maxillary teeth are of especial interest because of the manner in which their surfaces are worn. This does not produce a flat surface as in many other cricetines, but effects a median antero-posterior trough bounded on either side by the series of principal cusps. Conceivably this might be due to some ontogenetic or environmental basis in the single individual at hand, but it seems more probable that it indicates an insectivorous or otherwise peculiar food habit.

This genus does not fall readily into any well known group of cricetines. For the present it seems necessary to regard it as unique. When series of specimens are studied, including young with newly cut teeth, further light on it may be obtained. Beyond this, increased knowledge of extinct cricetines may be helpful.

The name *Punomys* is chosen for its brevity and euphony rather than its classical purity. It refers to the *puna* or treeless zone of the higher parts of Peru and Bolivia where this and a few other mammals exist at higher altitudes than those of any other part of the world.

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THE RACES OF THE OCELOT AND MARGAY IN MIDDLE AMERICA

By E. A. Goldman

In "The Races of the Ocelot and the Margay" Pocock (Zool. Ser., Field Mus. Nat. Hist., vol. 27, pub. 511, pp. 319–369, Dec. 8, 1941) records the results of "An effort to disentangle some of the knots of difficulties in the determination and distribution of the described local races of two American tiger cats . . . ." His paper has been the chief incentive to the writer to undertake at the present time further elucidation of the geographic races in Middle America, especially in view of lack of agreement with Pocock's disposition of some of the "knots" in the process of disentanglement.

These cats have been in urgent need of further revision and they remain imperfectly known, owing in part to the need for more ample material, especially to fill gaps in the known ranges of subspecies.

The ocelot appears to be fairly common throughout most of its range in Middle America, but the margay which is similarly dispersed, is a much rarer animal. A third group of very small tiger cats extends north from South America and is represented in Costa Rica by the form currently recognized as *Felis pardinoides oncilla*. It requires no consideration in this connection.

On the basis of extremely scanty specimen material and statements from literature, Pocock has arrived at conclusions regarding Middle American tiger cats that are obviously at variance in several particulars with the facts as shown by the limited, but more ample number of specimens available in American museums. Of *Felis pardalis pardalis* Linné, of Veracruz, he says (*op. cit.*, p. 343): "The published information about this race is meager and unsatisfactory. There are no specimens in the British Museum, apart perhaps from a skin, without skull, doubtfully assigned to it, from Dueñas, Guatemala. . . ." Then follows a description of this skin, statements from literature, and an attempt to justify the placing of *Felis pardalis nelsoni* of Colima, western Mexico, in the synonymy of typical *pardalis*. In describing two new ocelots from Mexico (Jour. Mamm., vol. 6, pp. 122–124, May 12, 1925) I did not mention all of the material used for comparison, but pointed out how the great wedge formed by the Mexican highlands splits the northern part of the range of this essentially tropical group in a manner bearing significantly on subspeciation. *Felis pardalis nelsoni* was based on 5 skins and skulls from Colima, supplemented by 15, mainly skins, from Guerrero and Oaxaca. These were compared with 6 skins and 10 skulls, including adults of both sexes from Veracruz, and other specimens believed to represent typical *pardalis*.

With discussion similarly unconvincing to me Pocock (*op. cit.*, p. 346) assigns *Felis pardalis sonoriensis* of Sonora to the synonymy of *Leopardus pardalis griseus*. *Leopardus griseus* was briefly described by Gray (Ann. Mag. Nat. Hist., vol. 10, p. 260, 1842) as from "Central America." Twenty-five years later Gray (Proc. Zool. Soc. London, 1867, p. 270) in notes on the skulls of the Felidae listed the species as *Felis grisea* and the habitat was recorded as Guate-

mala. The dimensions of the skull were given as length $5\frac{1}{8}$ inches; width $3\frac{3}{8}$ inches. On page 403 in the same volume the animal was more fully described, and he said: "My *Leopardus griseus* differs from the other Ocelots in having a grey fur with whitish sides." Two years later still Gray (Cat. Carn. Pach. Edent. Mamm. 1869, p. 19) again listed *Felis grisea*, with Guatemala as habitat. *Felis picta*, originally described by him as *Leopardus pictus* on the same page with *Leopardus griseus*, and like it ascribed to Central America, retained its habitat designation unchanged. In a review of the nomenclature of the ocelots Mearns (Proc. U. S. Nat. Mus., vol. 25, p. 245, Sept. 17, 1902) refers to Gray's statement that *Leopardus griseus* came from Guatemala and says: "I am unable to identify it with any of the forms I have examined." In a more complete treatment of the group: "Notes on the Synonymy and Nomenclature of the Smaller Tiger Cats of Tropical America," J. A. Allen (Bull. Amer. Mus. Nat. Hist., vol. 41, p. 345, Oct. 3, 1919) says: "Two names [*Leopardus griseus* and *Leopardus pictus*] had been given to ocelots of the *pardalis* group from Central America previous to Mearns' description of his *Felis costaricensis*, but they prove very difficult to identify and have thus far been held in abeyance." *Leopardus pictus* is assigned by Pocock (*op. cit.*, p. 322) to the synonymy of *Leopardus pardalis brasiliensis* Oken.

As the skin and skull of the type of *Leopardus griseus* are still extant, the name cannot, of course, be ignored. Pocock remarks (*op. cit.*, p. 346) that he can find no justification for Gray's statement in 1867 that the type came from Guatemala. Gray repeated the statement in 1869, but did not revise the habitat data for *Leopardus pictus*, described with *griseus* from "Central America," and it seems reasonable to assume that some additional information regarding the type locality may have been received by him. Some support for a conclusion that *griseus* came from Guatemala is the close approach of the skull of the type, an adult female, in total length (126 mm) as given by Pocock (*op. cit.*, p. 348), to that of a female about full grown (total length, 125.8 mm) in the American Museum of Natural History, from Finca Cipres, altitude about 2,000 feet, at the base of the Volcan Zunil, some 9 miles from Mazatenango, southwestern Guatemala. The Finca Cipres specimen and another in the same museum from Finca El Espino, altitude 150 feet, 15 miles south of Mazatenango, examined by me, were recorded as *Felis pardalis pardalis* by Goodwin (Bull. Amer. Mus. Nat. Hist., vol. 48, p. 22, Dec. 12, 1934). They agree closely not only in color but in size and cranial details with examples from Veracruz. In treating these specimens Goodwin mentioned the possibility of relationship to *Leopardus griseus* of Gray, which has proven to be "difficult to identify." Pocock, on the other hand, associates the type of *griseus* with material from Mazatlan, Sinaloa. Detailed comparisons are made and he says (*op. cit.*, p. 348): "The closeness of the likeness in shape and dimensions between the adult female skulls of the type *griseus* and of the example from Mazatlan is quite unusual even in skulls of the same sex, race, and locality." In a group of four fully mature female skulls, however, including two old adults from Escuinapa, about 50 miles southeast of Mazatlan, Sinaloa, among those examined by me in the American Museum

of Natural History the average total length is 118.5 mm and the extremes 115.5 to 122.5 mm. The total number of specimens available for comparison from Escuinapa is 24. These include old adults of both sexes and afford a fairly clear idea of the scope of individual variation. The series appears to be referable to *nelsoni* which doubtless passes into *sonoriensis* not far to the northward. Typical *sonoriensis* from beyond the northern limit of the Tropical Zone is still smaller. It may be pointed out that the skull of the fully adult male type of *sonoriensis* measures only 125.8 mm in total length, which is slightly less than this dimension (126 mm) in the female type of *griseus*. When the sex disparity in size is considered the significance of this difference becomes apparent. It is true that ocelots from the northern ends of the range of the group average grayer than those from farther south, but individual variation in color and arrangement of spots is remarkable everywhere. Not only are there no two individuals exactly alike, but the spots differ in detail from the median line down over the two sides of the same animal. Selected specimens from such widely separated regions as Veracruz, Guatemala, Sonora and Texas, representing three geographic races, are practically indistinguishable in grayish ground color. As further evidence in regard to color, Hamilton Smith's *Felis ocelot* No. 3 was based on a pale specimen called *Felis griffithii* by Fischer in 1830, and renamed *Felis canescens* by Swainson in 1838. These names are properly treated by Pocock as synonyms of typical *pardalis*. The color of the skin of the type of *griseus* which, as Pocock remarks, is "a century old and was formerly exhibited as a mounted specimen" can, therefore, hardly be accepted as diagnostic. Three skulls of adult females of *pardalis* range from 121.5 to 132.5 mm in total length. In the apparent absence of any known diagnostic character, or more definite information in regard to the type locality for *griseus*, Guatemala should apparently be accepted as the type region and the name may be placed in the synonymy of typical *pardalis*.

The ocelot is very similar to the margay in spotted pattern of coloration, but is much larger, more robust, with a shorter tail. The skull is more angular and massive, with a more prominent sagittal crest extending normally to the frontals. The two species have been treated by some authors, including Pocock, as generically different from *Felis*. In the more essential cranial characters, however, the differences from *Felis* are so narrowly quantitative instead of qualitative that generic recognition seems unwarranted. Possibly the differential color pattern may justify the use of *Leopardus* as a subgeneric name.

Among the unidentifiable or not clearly assignable names that may be associated with members of the *Felis pardalis* group are the following:

1792. *Felis mexicana* Kerr, Anim. King. no. 274, p. 151, 1792. Based on Pennant's account, and that in turn in part on the Tlalocelotl of Hernandez. Regarded as not determinable by Allen (Bull. Amer. Mus. Nat. Hist., vol. 7, p. 188, June 20, 1895).

1816. *Felis mexicana* Desmarest, Nouv. Dict. d'Hist. Nat., vol. 6, p. 112, 1816 edition [original date of publication about Feb. 4, 1803—See Osgood, Proc. Biol. Soc. Washington, vol. 27, p. 3, Feb. 2, 1914]. Based on the "Chat Sauvage de la Nouvelle Espagne" of Buffon (Hist. Nat., Sup., vol. 3, p. 227, pl. 43, 1776), which might be confused with the ocelot. Buffon himself (*op. cit.*, p. 228) re-

garded this as the same as the Serval, described and figured in his earlier work (Hist. Nat., vol. 13, p. 236, pl. 34, 1765).

1816. *P[anthera] mexicana* Oken. Lehrb. der Naturgesch., theil 3, abt. 2, p. 1054, 1816. Under this name Oken listed the "Tlaco-Ozelotl, Catus-Pardus mexicanus," "Panthera americana" and "F. pardalis." Apparently associated with the last mentioned he says "Die alten Könige von Mexico hatten dieses Thier um den Thron liegen." The next paragraph under the same heading, however, begins with "Jaguar (ist Tlaco-Ocelotl)." Aside from this apparent confusion of the ocelot with the jaguar the name is preoccupied by *Felis mexicana* Kerr (1792) and *Felis mexicana* Desmarest (1816).

1842. *Felis pseudopardalis* Boitard, Jardin des Plantes Description et Moeurs des Mammiferes, etc., p. 187, 1842. Based on the Ocelot du Mexique figured by Buffon (Hist. Nat. t. 9, pl. 18, 1761) and *Felis onca* by Schreber (Saug. pl. C 2, 1775). Although the name *Felis onca* appears on Schreber's plate, the heavy longitudinal stripe on the nape in the crude illustration conforms more closely to the color pattern of the ocelot. In regard to locality he says: "Il habite le Mexique et la baie of Campeche?" This name was treated by Mearns (Proc. U. S. Nat. Mus., vol. 25, p. 240, 1903) as a synonym of *Felis pardalis*.

1860. *Felis pardalis minimus* Wilson, Proc. Acad. Nat. Sci. Phila., p. 82, 1860. This name was based on a very small kitten from Realejo, Nicaragua, which was permitted its liberty on the deck of a ship. One morning its absence was noted and it became apparent that the animal was lost overboard during the night. While the name was assigned to the *pardalis* group there seems to be no means of determining whether it was applied to an ocelot or a margay.

1911. *Felis buffoni* and *Felis mexicana* Brass, Aus dem Reiche del-Pelze, p. 412, Apr. 1911. These names were proposed with color descriptions of spotted Mexican cats, presumably ocelots. No definite localities are given and they are evidently based on individual color variations of which there may be many in the same locality. *Felis mexicana* had already been used several times. Both names are unidentifiable.

The present review of the Middle American ocelots is based on studies of a total of 111 specimens. Of this number 24 were skins without skulls, and 25 were skulls without skins. The specimens, unless otherwise stated, are in the U. S. National Museum, including the Biological Surveys collection.

For the privilege of examining material and other courtesies, I am indebted to Harold E. Anthony, George G. Goodwin, and T. Donald Carter, American Museum of Natural History, New York.

The races of the ocelot inhabiting Middle America appear to be recognizable, as follows:

Felis pardalis pardalis Linné

Veracruz Ocelot

[*Felis*] *pardalis* Linné, Syst. Nat., ed. 10, vol. 1, p. 42, 1758. Based on the Cato-pardus Mexicanus of Hernandez.

Felis ocelot Link, Beitr. Zool., 2, p. 90, 1795. (See Osgood, Jour. Mamm., vol. 1, no. 2, p. 88, Mar. 2, 1920).

Felis ocelot No. 3, Hamilton Smith in Griffith's Anim. Kingd., Mamm., vol. 2, p. 476, pl., 1827.

Felis griffithii Fischer, Synop. Mamm. Addend., Emend. et Index, p. 369, 1830. Based on a pale specimen in the Bullock Collection, probably from Veracruz, Mexico.

Felis canescens Swainson, Anim. in Menog., p. 118, 1838. (= *Felis ocelot* No. 3, Hamilton Smith.)

Leopardus griseus Gray, Ann. Mag. Nat. Hist., vol. 10, p. 260, 1842. From "Central America." Ascribed to Guatemala by Gray, Proc. Zool. Soc. London, 1867, p. 270.

Felis pardalis True, Proc. U. S. Nat. Mus., vol. 7, p. 610 (1884) 1885.

Felis pardalis pardalis J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 22, p. 221, July 25, 1906.

Felis griffithii Osgood, Jour. Mamm., vol. 1, p. 90, Mar. 2, 1920.

Leopardus pardalis pardalis J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 41, p. 345, Oct. 3, 1919.

Leopardus pardalis pardalis Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, Pub. 511, p. 342, Dec. 8, 1941.

Type locality.—State of Veracruz, Mexico.

Distribution.—Tropical lowlands and eastern slopes of the interior plateau in Veracruz, south across the Isthmus of Tehuantepec and east through Tabasco, Chiapas, and Guatemala to Honduras (Balfate).

General characters.—Size medium or rather large; general body color, size, shape, and arrangement of rosettes variable, as is usual in the group; interspaces between rosettes over dorsum varying from buffy gray to near "cinnamon" (Ridgway, 1912); skull massive; brain case broad; zygomata widely spread posteriorly, narrowed anteriorly; lambdoid crest moderately upturned; dentition moderate. Size usually smaller than in *mearnsi* of Costa Rica; color averaging paler and grayer, less tawny; skull smaller, less elongated; lambdoid crest more upturned. Similar in size but tending to be larger than *albescens* of eastern Texas and neighboring territory; pelage shorter; colors usually darker, cinnamon buffy or "cinnamon" instead of plainer grayish tones tending to prevail; interspaces between rosettes usually broader; skull similar in general form; lambdoid crest less upturned; dentition heavier. Size larger than *nelsoni*; color about the same; skull usually distinctly larger; zygomata more converging anteriorly, the sides less evenly bowed outward; dentition heavier.

Measurements.—A male approaching full grown, but sagittal crest slightly developed, from Catemaco, Veracruz: Total length, 1130 mm; tail vertebrae, 375; hind foot, 164. An adult male from Finca El Espino, Guatemala: 1125; 334; 170. An adult or nearly adult female from Champoton, Campeche: 1080; 360; 155. *Skull:* An old male from Catemaco, Veracruz, and a younger but nearly full grown male from Mirador, Veracruz, respectively: Greatest length, 150.4, 144.4; condylobasal length, 137.5, 134.5; zygomatic breadth, 102.4, 90.5; squamosal constriction, 57.4, 54.7; interorbital breadth, 26, 25; postorbital constriction, 27.5, 26; maxillary tooth row, crown length to back of carnassial, 41.5, 41.8; upper carnassial, crown length (outer side), 15.3, 16.4. An adult male (fronto-parietal suture closed and sagittal crest moderately developed) from Finca El Espino, 15 miles south of Mazatenango, Guatemala: Greatest length, 140.2; condylobasal length, 129.2; zygomatic breadth, 94.5; squamosal constriction, 51, interorbital breadth, 27.1; postorbital constriction, 31.4; maxillary tooth row, crown length to back of carnassial, 42; upper carnassial, crown length (outer side), 17.1. An adult but not very old female from Buena Vista, Veracruz, and an old female from Perez, Veracruz, respectively: Greatest length, 121.5, 132.5; condylobasal length, 113, 122; zygomatic breadth, 87.2, 91.4; squamosal constriction, 47, 53.2; interorbital breadth, 21.7, 25.5; postorbital constriction, 29.4, 29; maxillary tooth row, 38.7, 38; upper carnassial, 15.3, 15.2. A female about full-grown, but frontoparietal suture open, from Finca Cipres, base of Volcan Zunil, Guatemala: Greatest length, 125.8; condylobasal length, 117; squamosal constriction, 49.9; interorbital breadth, 24.8; postorbital constriction, 33.4; maxillary tooth row, crown length to back of carnassial, 39.1; upper carnassial, crown length (outer side), 15.1.

Remarks.—*Felis pardalis* was based by Linné on the Cato-pardus mexicanus of Hernandez, from Mexico. The type region was more definitely assigned as Veracruz by J. A. Allen (Bull. Amer. Mus. Nat. Hist., vol. 41, p. 345, Oct. 3, 1919). From the tropical lowlands in Veracruz the typical subspecies ranges up over the adjoining mountain slopes, but is absent on the high plateau of the interior. From the lowlands across the Isthmus of Tehuantepec it extends eastward at least to Honduras. It is possible that ample material from Guatemala may show that *griseus*, ascribed to that country by Gray, is a recognizable regional race; but

the few specimens examined do not appear to differ in any essential respect from typical *pardalis*. The ocelots of Middle America diminish progressively in size from south to north, especially along the Pacific coast. The typical subspecies is, therefore, intermediate in geographic range, as well as in detailed characters, between more northern and southern races.

Specimens examined.—Total number, 20, as follows: **Campeche:** Campeche, 2 (skins without skulls); La Tuxpeña, Champoton, 2 (skins without skulls). **Guatemala:** Finca Cipres (base of Volcan Zunil, about 9 miles from Mazatenango), 1 (Amer. Mus. Nat. Hist.); Finca El Espino (15 miles south of Mazatenango), 1 (Amer. Mus. Nat. Hist.). **Honduras:** Archaga, (20 Kilometers north of Tegucigalpa), 2 (Amer. Mus. Nat. Hist.); Balfate, Colon, 1 (skull only). **Oaxaca:** Huilotepec (8 miles southeast of Tehuantepec), 1. **Tabasco:** Teapa, 1. **Veracruz:** Catemaco, 3 (2 skulls without skins); Mirador, 1 (skull only); Perez, 5.

Felis pardalis mearnsi Allen

Costa Rican Ocelot

Felis costaricensis Mearns, Proc. U. S. Nat. Mus., vol. 25, p. 245, Sept. 17, 1902. Not *Felis bangsi costaricensis* Merriam, 1901, proposed for a puma.

Felis mearnsi J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 20, p. 71, Feb. 29, 1904. (Substitute for *Felis costaricensis* Mearns, preoccupied.)

Felis pardalis mearnsi J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 20, p. 71, Feb. 29, 1904.

Leopardus pardalis mearnsi J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 41, Oct. 3, 1919.

Type locality.—Talamanca, northeastern Costa Rica. Type of *Felis costaricensis* (= *F. p. mearnsi*), no. 14180, old male, skull only, U. S. National Museum; collected by W. M. Gabb.

Distribution.—Panama, Costa Rica, and northward probably to Nicaragua.

General characters.—Size, as indicated by skulls, averaging the largest of the Middle American subspecies; color dark, the spaces within and between rosettes along median line of dorsum, in Panama specimens at least, more or less distinctly "ochraceous-tawny"; skull relatively narrow and elongated; lambdoid crest not distinctly upturned; dentition heavy. Similar in general to *pardalis* of Veracruz, but usually larger; upper parts more distinctly tawny instead of grayish in ground color; skull usually larger, more elongated; lambdoid crest less upturned; dentition similar, but rather heavy. Similar in size to *Felis pardalis aequatorialis* of northern Ecuador, but ground color of upper parts less tawny than in the type; skull also similar, but brain case narrower than in the type specimen.

Measurements.—An adult male from Gatun, Canal Zone: Total length, 1230 mm; tail vertebrae, 355; hind food, 151. Two adult females from Gatun, Canal Zone, respectively: Total length, 1095, 1110; tail vertebrae, 350, 355; hind foot, 146, 149. *Skull:* Type and an old male from Punta de Peña, Bocas del Toro, Panama, respectively: Greatest length, 158, 156.4; condylobasal length, 146.3, 143.5; zygomatic breadth, 106.2, 100.5; squamosal constriction, 57.8, 56.2; interorbital breadth, 29.2, 27.3; postorbital constriction, 32, 26.3; maxillary tooth row, crown length to back of carnassial, 45.2, 47.1; upper carnassial, crown length (outer side), 16.8, 18.2. An adult female from Isthmus of Panama: Greatest length, 140.7; condylobasal length, 126.8; zygomatic breadth, 96.4; squamosal constriction, 54.4; interorbital breadth, 29.8; postorbital constriction, 27.8; maxillary tooth row, crown length to back of carnassial, 39.6; upper carnassial, crown length (outer side), 15.7.

Remarks.—*F. p. mearnsi* doubtless passes into *aequatorialis* on the east in Colombia, as suggested by comparison with the type, and remarks by Pocock (*op. cit.*, p. 335) and others. In Middle America close alliance with typical *pardalis* is evident, and the two forms probably intergrade in Nicaragua.

Specimens examined.—Total number, 15, as follows: **Costa Rica:** Pacific side, 1 (skull only); Talamanca (type locality), 5 (skulls only). **Panama:** Boqueron, 1 (Amer. Mus. Nat. Hist.); Gatun, 3; "Isthmus of Darien", 1; Isthmus of Panama, 1 (skull only); Mount Pirri, 1 (skull only); Punta de Peña, Bocas del Toro, 1 (skull only), Real de Santa Maria, 1 (Amer. Mus. Nat. Hist.).

Felis pardalis nelsoni Goldman

Colima Ocelot

Felis pardalis nelsoni Goldman, Jour. Mamm., vol. 6, no. 2, p. 122, May 12, 1925.

Type locality.—Manzanillo, Colima, Mexico (altitude 50 feet). Type no. $\frac{32642}{44565}$, old male, skin and skull, U. S. National Museum (Biological Surveys collection); collected by E. W. Nelson, February 11, 1892.

Distribution.—Pacific coastal lowlands and western slope of the mountains of the interior from southern Oaxaca (Puerto Angel) north to southern Sinaloa (Escuinapa). Intergradation with *sonoriensis* farther north, and with typical *pardalis* on the south may safely be assumed.

General characters.—Similar in general to *Felis pardalis pardalis* of Veracruz, but smaller; color averaging about the same; skull usually smaller; zygomata more evenly bowed outward, the sides more nearly parallel, less abruptly converging anteriorly; dentition lighter. Size larger than *sonoriensis* of Sonora; general color somewhat darker, the black markings above and below separated by narrower light interspaces, black cervical stripes usually broader; skull larger, the brain case more elongated; frontal region less elevated; zygomata rather narrowly spreading posteriorly, without marked convergence anteriorly, and teeth small, much as in *sonoriensis*.

Measurements.—Type, an old male, and one of similar age with high sagittal crest from Papayo, Guerrero, respectively: Total length, 1140, 1120 mm; tail vertebrae, 362, 372; hind foot, 166, 157. Two males nearing maturity but sagittal crest low, from type locality, respectively: Total length, 1002, 1060; tail vertebrae, 350, 310; hind food, 155, 143. A male nearing maturity but sagittal crest low, from Armeria, Colima: Total length, 1140; tail vertebrae, 400; hind foot, 170. An adult female topotype and one from Puerto Angel, Oaxaca, respectively: Total length, 995, 1000; tail vertebrae, 310, 325; hind foot, 155, 143. *Skull:* Type, an old male, and one of similar age from Papayo, Guerrero, respectively: Greatest length, 143.8, 141; condylobasal length, 131.4, 130.3; zygomatic breadth, 95.9, ——; squamosal constriction, 51.2, ——; interorbital breadth, 25.4, 25.4; postorbital constriction, 24.8, 30.5; maxillary tooth row, crown length to back of carnassial, 38.8, 40.6; upper carnassial, crown length (outer side), 14.7, 15. An adult female topotype and one of similar age from Puerto Angel, Oaxaca, respectively: Greatest length, 120, 121.8; condylobasal length, 112.8, 112.5; zygomatic breadth, 83.3, 82.5; squamosal constriction, 47.7, 50.5; interorbital breadth, 23, 23.8; postorbital constriction, 34.5, 34.5; maxillary tooth row, crown length to back of carnassial, 37; upper carnassial, crown length (outer side), 14.1, 15.8.

Remarks.—*F. p. nelsoni* occupies the tropical strip extending north along the western coast of Mexico. It appears to give way to *sonoriensis* near the point where the northward range of the group passes into the arid Lower Sonoran division of the Lower Austral life zone.

Specimens examined.—Total number, 42, as follows: **Colima:** Armeria, 1; Manzanillo (type locality), 4. **Guerrero:** Acapulco, 4 (skins only); Coyuca, 6 (skins only); Omilteme, 1; Papayo, 1. **Oaxaca:** Puerto Angel, 1. **Sinaloa:** Escuinapa, 24 (5 skins without skulls; 2 skulls without skins) (Amer. Mus. Nat. Hist.).

Felis pardalis sonoriensis Goldman

Sonora Ocelot

Felis pardalis sonoriensis Goldman, Jour. Mamm., vol. 6, no. 2, p. 123, May 12, 1925.

Type locality.—Camoa, Rio Mayo, Sonora, Mexico (altitude 800 feet). Type no. 96216, adult male, skin and skull, U. S. National Museum (Biological Surveys collection); collected by E. A. Goldman, December 3, 1898.

Distribution.—Warmer western slopes of the Sierra Madre from southern Sonora, and probably northern Sinaloa, north to southeastern Arizona; formerly as far north as Fort Verde, Arizona; absent in the arid plains region of western Sonora.

General characters.—Most closely allied to *nelsoni*, but averaging still smaller; general color somewhat paler, the black dorsal and ventral markings more widely spaced by lighter areas; black cervical stripes usually narrower; skull smaller, the brain case relatively shorter, more rounded; frontal region more elevated; zygomata narrowly spreading posteriorly, without marked convergence anteriorly, and teeth small, much as in *nelsoni*. Similar in color to *albescens* of eastern Texas, but decidedly smaller and owing to isolation no very close comparison is required. Aside from smaller size the skull is relatively shorter, more rounded in form than that of *albescens*; zygomata less convergent anteriorly; supraoccipital crest usually less upturned; dentition light, much as in *albescens*.

Measurements.—Type and two male topotypes, all apparently mature, but sagittal crests low, respectively: Total length, 980, 1040, 1015 mm; tail vertebrae, 320, 351, 325; hind foot, 148, 149, 149. *Skull*: Three males just described, respectively: Greatest length, 125.3, 121, 123.3; condylobasal length, 115.6, 114.8, 114; zygomatic breadth, 85.9, 83.5, 82; squamosal constriction, 48.6, 47.7, 47; interorbital breadth, 24.2, 23.8, 21.8; postorbital constriction, 32.5, 29.3, 29.8; maxillary tooth row, crown length to back of carnassial, 35.5, 36.6, 38; upper carnassial, crown length (outer side), 13.2, 14.8, 15.5.

Remarks.—The range of *sonoriensis* marks the northern limit, on the western side of the continent, of an intergrading chain of geographic races extending from South America. This race, the smallest of the ocelots of Middle America, presents a marked contrast in size and color with the much larger more richly-hued subspecies, *mearnsi*, of Costa Rica and Panama.

Specimens examined.—Total number, 5, as follows: **Arizona:** Fort Verde, 1 (skin only) (Amer. Mus. Nat. Hist.). **Sonora:** Camoa (type locality), 4.

Felis pardalis albescens Pucheran

Texas Ocelot

Felis albescens Pucheran, in Geoffroy St. Hilaire, Voy. Venus, Zool. Mamm., p. 149, Atlas, pl. 8, 1855.

Felis limitis Mearns, Proc. Biol. Soc. Washington, vol. 14, p. 146, Aug. 9, 1901. Type from Brownsville, Cameron County, Tex.

Felis pardalis limitis Bailey, North Amer. Fauna, no. 25, p. 66, Oct. 24, 1905.

Felis ludoviciana Brass, Aus dem Reiche der Pelze, p. 411, April, 1911. "In Louisiana, Arkansas, und Texas wird es durch eine andere verwandte Art vertreten, *Felis ludoviciana* oder *limitis*."

Felis pardalis albescens J. A. Allen, Bull, Amer. Mus. Nat. Hist., vol. 22, p. 219, 1906.

Leopardus pardalis griffithii J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 41, p. 345, Oct. 3, 1919. (Part.)

Leopardus pardalis albescens Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, Pub. 511, p. 350, Dec. 8, 1941.

Type locality.—Arkansas ("de l'état d'Arkansas, dans la Louisiane").

Distribution.—Formerly parts of Arkansas and probably the present state of Louisiana; still ranging in eastern and southern Texas and south into the northeastern states of Mexico (Soto la Marina, Tamaulipas). The intergradation of *albescens* with typical *pardalis* on the south and isolation from *sonoriensis* on the west is indicated by specimens compared.

General characters.—Similar in size but averaging somewhat smaller than typical *pardalis* of Veracruz; pelage longer; colors usually paler, grayish instead of cinnamon-buffy or "cinnamon" tones tending to prevail; black markings somewhat reduced, leaving wider interspaces; skull very similar in general form; lambdoid crest usually more extended laterally to form broader supraoccipital shelves with edges more upturned; dentition lighter. Similar in color to *sonoriensis* of Sonora, but owing to isolation no very close comparison is required. Aside from larger size, the skull is more elongated than that of *sonoriensis*; zygomata more convergent anteriorly; lambdoid crest usually more upturned; dentition light, much as in *sonoriensis*.

Measurements.—Two males apparently mature but with sagittal crests low, from Browns-

ville, Texas, respectively: Total length 1188, 1080; tail vertebrae, 380, 330; hind foot, 155, 160. Two adult females from Brownsville, Texas, respectively: Total length, 940, 920; tail vertebrae, 270, 300; hind foot, 140, 130. *Skull:* Three males, apparently mature but with sagittal crests low, from Angleton, Texas, respectively: Greatest length, 142.7, 136.7, 135.7; condylobasal length, 132.2, 126, 124.9; zygomatic breadth, 90.3, 91, 93.2; squamosal constriction, 58.4, 54.8, 54.2; interorbital breadth, 26.5, 26.8, 26.9; postorbital constriction, 28.6, 29.3, 32.4; maxillary tooth row, crown length to back of carnassial, 40.6, 39.5, 38; upper carnassial, crown length (outer side), 15.5, 14.7, 14.4. Two adult females from Bay City and Brownsville, Texas, respectively: Greatest length, 122.8, 120.9; condylobasal length, 114.7, 111.3; zygomatic breadth, 87.7, 86.5; squamosal constriction, 51.8, 49.8; interorbital breadth, 24.7, 22.6; postorbital constriction, 31, 33.7; maxillary tooth row, 36, 35.1; upper carnassial, crown length (outer side), 13.8, 14.2.

Remarks.—The subspecies *albescens* represents the northern limit of the ocelot east of the continental divide, which interposes a barrier between eastern and western northward extensions of the general range of the species in northern Mexico. Bone carving, believed to be of the ocelot, from a mound of the Mound Builders in Ross County, south-central Ohio, suggests that the range of the species may formerly have extended considerably farther north (See Moorehead, Anth. Ser. Field, Mus. Nat. Hist., vol. 6, no. 5, Pub. 211, p. 159, 1922). The resemblance of *albescens* to *sonoriensis* in color may suggest close relationship, but differences in size and cranial details are quite trenchant. *Felis limitis* Mearns was proposed as a substitute name for *albescens* which was believed to be untenable, but the validity of the latter has since been established.

Specimens examined.—Total number, 29, as follows: **Texas:** Alamo de Cesarea Ranch (between Marfa and Terlingua), Brewster County, 1 (skin only); Angleton (18 miles west), 3 (2 skulls without skins); Bay City (18 miles east), 1; Brownsville, 10 (4 skulls without skins); Eagle Pass, 1; Raymondville (20 miles northeast), 2. King Ranch, Kleberg County, 2 (skins only) (Stanley P. Young Coll.). **Tamaulipas:** Matamoros, 4 (skulls only); Soto la Marina, 5 (skins only).

The margay, *Felis wiedii*, is a species of wide distribution from southern Brazil and parts of Bolivia north throughout the warmer parts of Middle America to northern Mexico and southern Texas. The northern end of its range, like that of the ocelot, appears to be bifurcated by the southern extension of the interior plateau. As in other American cats of wide dispersal, notably the ocelot, jaguar, and puma, the species is subdivisible into geographic races. The races are little known, however, as too few specimens have appeared in museum collections. Only two examples of the margay were obtained by E. W. Nelson and the writer, in making a general collection of more than 15,000 mammals, in the course of biological investigations extending, during 12 years, into every state and territory on the mainland of Mexico. It is possible, however, that special efforts to obtain specimens by modern methods will reveal that the species is not so rare as is generally believed.

The reference by Pocock of the races of the margay of Middle America, as well as South America, to *Felis wiedii* is a contribution toward the clarification of specific relationships not previously well understood.

The following treatment of subspecies should be regarded as provisional.

Felis wiedii pirrensis Goldman

Panama Margay

Felis pirrensis Goldman, Smiths. Misc. Coll., vol. 63, no. 5, p. 4, Mar. 14, 1914.
Leopardus wiedii pirrensis Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, Pub. 511, p. 360, Dec. 8, 1941.

Type locality.—Cana, eastern Panama (altitude 2,000 feet). Type no. 179162, adult female, skin and skull, U. S. National Museum (Biological Surveys collection); collected by E. A. Goldman, March 22, 1912.

Distribution.—Eastern Panama, and south perhaps to Ecuador and Peru.

General characters.—Size large; ground color of upper parts in type specimen "ochraceous tawny" (Ridgway, 1912), nearly uniform from nape to base of tail, becoming somewhat paler on head and paling through "cinnamon-buff" to "pinkish buff" along lower part of sides; skull of type large and elongated, the vault of brain case highest near frontoparietal suture; frontal region rather depressed and sloping downward anteriorly; zygomata narrowly spreading posteriorly, the squamosal arms not strongly bowed outward; orbits prominent, the jugals broad and laterally expanded; palate narrow. Similar in general to *nicaraguae* of Nicaragua, but apparently somewhat larger; color pattern very similar, with the differences in detail usual in the group, but spaces between black markings over dorsum more "ochraceous-tawny"; skull larger, more elongated; brain case narrow throughout, the vault higher, more narrowly convex in transverse section; zygomata relatively less strongly bowed outward posteriorly, the sides more nearly parallel; dentition similar.

Measurements (type).—Total length, 963 mm; tail vertebrae, 440; hind foot, 131.5. Skull: Greatest length, 100.6; condylobasal length, 95.8; zygomatic breadth, 63; breadth of brain case, 45.7; squamosal constriction, 40.9; interorbital breadth, 18.7; postorbital constriction, 33.9; maxillary tooth row to back of carnassial, 29.4; upper carnassial, crown length (outer side), 11.8.

Remarks.—The skull of the type of *pirrensis*, a female, is considerably larger than that of an adult female specimen of *nicaraguae* from Matagalpa, Nicaragua. The adult male type of *nicaraguae*, however, is larger than the female type of *pirrensis*. The comparative size of the two remains, therefore, somewhat uncertain. *F. p. nicaraguae* was placed by Pocock (*op. cit.*, p. 360) in the synonymy of *pirrensis*, but seems to differ in color and cranial details as pointed out. The same treatment of *Felis (Margay) glaucula ludovici* Lönnberg from Pichincha, Ecuador, was accorded by him. No South American material has been considered by me in this review.

Specimens examined.—One, the type.

Felis wiedii nicaraguae (Allen)

Nicaragua Margay

Margay glaucula nicaraguae Allen, Bull, Amer. Mus. Nat. Hist., vol. 41, p. 357, Oct. 3, 1919.
Felis glaucula nicaraguae Miller, North Amer. Rec. Mamm., Bull. 128, U. S. Nat. Mus., p. 156, 1923 (1924).

Type locality.—Volcan de Chinandega, western Nicaragua. Type no. 28957, adult male, American Museum of Natural History; collected by W. B. Richardson, August 20, 1908.

Distribution.—Nicaragua, Honduras, and Costa Rica.

General characters.—Similar in general to *pirrensis* of Panama, but apparently somewhat smaller; ground color less "ochraceous-tawny"; skull smaller, less elongated; brain case lower, more expanded posteriorly, the valt less narrowly convex in transverse section; zygomata more strongly bowed outward posteriorly, the sides more convergent anteriorly, dentition similar. Not unlike *salvinia* of Guatemala in color, but apparently larger.

Measurements.—Type (from original description, quoted in selected parts only): "Total length, 1260 mm; tail vertebrae, 510. Skull: Total length, 107; condylobasal length, 100.9; zygomatic breadth, 72.2; interorbital breadth, 19.2; upper carnassial, 12.4." An adult female from Matagalpa, Nicaragua: Condylobasal length, 89.2; zygomatic breadth, 6.6; breadth of brain case, 47.6; squamosal constriction, 40.8; interorbital breadth, 17; postorbital constriction, 35.2; maxillary tooth row to back of carnassial, 27.5; upper carnassial, crown length (outer side), 11.4. A female approaching full-grown, from Guimaca, Honduras: Greatest length, 89.7; condylobasal length, 87.9; zygomatic breadth, 60.3; breadth of brain case, 43.4; squamosal constriction, 37.8; interorbital breadth, 16.4; postorbital constriction, 30; maxillary tooth row, crown length to back of carnassial, 26.4; upper carnassial, crown length (outer side), 10.8.

Remarks.—The Nicaragua margay was placed by Pocock (Zool. Ser., Field Mus. Nat. Hist., vol. 27, p. 360, Dec. 8, 1941) in the synonymy of *pirrensis*, although no specimens from Nicaragua were examined by him. The very limited material available for comparison, however, indicates that they represent closely allied but recognizable geographic races. A female, apparently approaching full-grown, from Guaymaca, Tegueigalpa, south-central Honduras is small but probably referable to *nicaraguae*.

Specimens examined.—Five, from localities as follows: **Honduras:** Guaymaca, 1 (Amer. Mus. Nat. Hist.); Santa Barbara, 1 (Amer. Mus. Nat. Hist.). **Nicaragua:** Matagalpa, 1 (Amer. Mus. Nat. Hist.); Volcan de Chinandega, 1 (Amer. Mus. Nat. Hist.). **Costa Rica:** Cañas Gordas, 1 (Amer. Mus. Nat. Hist.).

Felis wiedii salvinia Pocock

Guatemala Margay

Leopardus wiedii salvinia Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, p. 366. Dec. 8, 1941.

Type locality.—Vera Paz, Guatemala, no. 1875.2.27.1, adult male, skin and skull, British Museum (Natural History); collected by O. Salvin.

Distribution.—Guatemala, and perhaps British Honduras.

General characters (from original description).—"Intermediate between *nicaraguae* and the western Mexican race *glaucula*, resembling the former very closely in color, but with a much smaller skull, about the same size as in *glaucula*.

"The type has the coat 16 mm. long on the back, 9 mm. on the nape. The color of the back is pale ochraceous tawny, matching almost exactly that of the specimen from Central America assigned to *nicaraguae*; the flanks are buff and the pattern on the sides consists mostly of isolated, irregular rosettes with narrowish dark brown rims and dull ochraceous centers, very much as in that specimen, but the rosettes are smaller and the centers paler and the black markings on the tail are not dominant over the pale interspaces. . . ."

Skull.—The skull of the type is evidently small and perhaps nearest in size to that of *yucatanica*.

Measurements (from original description).—". . . no flesh measurements were taken.

"The skull of the type, judging by its upper sutures, is fully adult. It has lost its lower occipital area, but its total length is 95 mm. and I infer from comparison with other skulls that its condylo-basal length was 88 or 89 mm., both this dimension and the total length being 12 mm. less than in the type of *nicaraguae*. Its width dimensions are also mostly less; but the cranium is unusually broad, nearly equaling half the length, namely, 46 mm as against 43 in the type of *nicaraguae*.

Remarks.—*F. w. salvinia* must be regarded as another imperfectly known form, owing to inadequate material for study. Aside from the type the describer records a specimen from Dueñas, Guatemala "too young to be worth measuring," and two skulls, without skins, from Belize, British Honduras, from the Zoological Society's Museum, marked "menagerie", are tentatively referred to it. The reliability of zoo specimens is always open to question for comparative purposes, owing to modification due to confinement. Most of the comparison is with *nicaraguae*, which had been placed by Pocock in the synonymy of *pirrensis*. The description of the type suggests that *salvinia* may be a rather small, dark form similar in size to *yucatanica*. A small female from Guaymaca, south-central Honduras, is provisionally referred to *nicaraguae*, but may possibly represent gradation toward *salvinia*. No specimens definitely assignable to this race have been examined by me.

Felis wiedii yucatanica Nelson and Goldman

Yucatan Margay

Felis glaucula yucatanica Nelson and Goldman, Jour. Mamm., vol. 12, no. 3, p. 304, Aug. 24, 1931.

Leopardus wiedii yucatanica Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, p. 368, Dec. 8, 1941.

Type locality.—Merida, northern Yucatan.

Distribution.—The peninsula of Yucatan and northern Chiapas; limits of range unknown.

General characters.—Distinguished by very pale buffy grayish ground color. Type decidedly paler than that of *oaxacensis*, with less dusky admixture along median line of dorsum, the enclosed markings narrower, more elongated, instead of broadly rounded. Skull of female from Tecpactan, Chiapas, compared with *oaxacensis*: Nasals still narrower posteriorly; dentition heavier, the upper carnassials broader. Contrasting still more widely in pale coloration with *nicaraguae* of Nicaragua. Dentition not unlike that of *nicaraguae*, but interpterygoid fossa narrower, and nasals narrower posteriorly.

Measurements.—Young female (permanent premolars not yet fully in place) from Tecpactan, Chiapas: Total length, 835 mm; tail vertebrae, 382; hind foot, 120. Skull (of preceding): Greatest length, 89.2; condylobasal length, 84.5; zygomatic breadth, 54.9; breadth of brain case, 44.2; squamosal constriction, 37.1; interorbital breadth, 14.7; postorbital constriction, 30.4; maxillary tooth row, crown length to back of carnassial, 27; upper carnassial, crown length (outer side), 11.8. Cranial measurements of an adult female from northern Yucatan in the British Museum have been recorded by Pocock (*op. cit.*, p. 369) as follows: Zygomatic breadth, 62; width of brain case, 45.

Remarks.—Pallid coloration associated with the general aridity of the climate distinguishes various mammals of the Yucatan peninsula region, in contrast with those of more humid sections farther south, and this geographic race of the margay appears to be no exception.

Specimens examined.—Two, as follows: **Chiapas**: Tecpactan, 1. **Yucatan**: Merida, 1 (skin only).

Felis wiedii oaxacensis Nelson and Goldman

Oaxaca Margay

Felis glaucula oaxacensis Nelson and Goldman, Jour. Mamm., vol. 12, no. 3, p. 303, Aug. 24, 1931.

Felis mexicana Saussure, Rev. Mag. Zool., 2 ser., t. 12, Jan. 1860. From Alvarado, Vera Cruz. (Name preoccupied by *Felis mexicana* Desmarest, 1816, for the Serval.)

Type locality.—Cerro San Felipe, near Oaxaca, Oaxaca, Mexico (altitude 10,000 feet). Type, no. 68169, adult male, skin and skull, U. S. National Museum (Biological Surveys collection); collected by Nelson and Goldman, August 31, 1894.

Distribution.—Oaxaca, and Veracruz; limits of range undetermined.

General characters.—Similar to *glaucula* of Jalisco; buffy gray and black color tones about the same, but pattern different, large, rounded rosettes with heavy black borders instead of narrower, more elongated markings tending to prevail over upper parts; skull very similar in general form, but nasals broader, more flattened and depressed anteriorly, narrower, more compressed posteriorly; auditory bullae smaller, less fully inflated; maxillary tooth row longer. Distinguished from *yucatanica* of Yucatan by darker color and apparently larger size.

Measurements.—Type: Total length, 910 mm; tail vertebrae, 368; hind foot, 130. Skull: Type, an adult male, and an adult, apparently female, from Cordoba, Veracruz, respectively: Greatest length, 95.7, 86.1; condylobasal length, 90.1, 82.7; zygomatic breadth, 67.4, 59.6; breadth of brain case, 44.5, 42.5; squamosal constriction, 39, 37.4; interorbital breadth, 17.9, 15.3; postorbital constriction, 33.5, 29; maxillary tooth row, crown length to back of carnassial, 29.4, 24.7; upper carnassial, crown length (outer side), 11.6, 9.5.

Remarks.—*F. w. oaxacensis* was described from a specimen taken at an elevation of 10,000 feet, near the summit of the Cerro San Felipe, a high mountain near Oaxaca. The record seems to represent an extreme in altitudinal range, and as the general drainage is toward the east it seems probable that this subspecies is generally distributed in the warm humid region including most of Veracruz. It was placed by Pocock (Zool. Ser., Field Mus. Nat. Hist., vol. 27, p. 367, Dec. 8, 1941) in the synonymy of *glaucula*, but the type and a specimen from

Cordoba, Veracruz, differ as indicated by two adults males from Los Masos, Jalisco, which are assumed to represent typical *glaucula*. As pointed out by Pocock, individual variation in color pattern in these cats covers an extensive range, but there seems to be some evidence that this variation, as in many other species, is within limits beyond which it does not usually pass; and geographic considerations should be given due weight, especially in the absence of ample material. Pocock (*op. cit.*, p. 367) refers to *glaucula* a skin labeled "Mexico" from the Bullock collection which he states is not so gray as the type, having a faint buff cast over the dorsal surface and in the centers of the rosettes, which have thick, blackish brown rims, coalescent into bands or isolated. As I have understood that the Bullock collection probably came from southeastern Mexico, and the thick rims of the rosettes suggest those of *oaxacensis*, it seems possible that this specimen should be referred to that form.

Specimens examined.—Two, the type and one from Cordoba, Veracruz.

Felis wiedii glaucula Thomas

Western Mexican Margay

Felis glaucula Thomas, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 235, August 1903.
Margay glaucula glaucula Allen, Bull. Amer. Mus. Nat. Hist., vol. 41, p. 357, Oct. 3, 1919.
Leopardus wiedii glaucula Pocock, Zool. Ser., Field Mus. Nat. Hist., vol. 27, p. 367, Dec. 8, 1941.

Type locality.—Beltran, Jalisco, Mexico. Type, no. 1890.1.4.1, female, skin and skull, British Museum; collected by W. Lloyd, April 25, 1889.

Distribution.—Western Mexico, from Jalisco north to southern Sinaloa; limits of range unknown.

General characters.—Similar to *oaxacensis* of Oaxaca; buffy gray and black color tones about the same, but pattern different, the enclosed areas on upper parts narrower, more elongated or confluent with comparatively narrow borders, instead of the large rounded rosettes and heavier black markings of the type of *oaxacensis*; skull similar in general form, but somewhat smaller; nasals narrower, more highly arched anteriorly, broader, less compressed posteriorly; auditory bullae larger, more fully inflated; maxillary tooth row shorter.

Measurements.—The accuracy of the external measurements of the type, as given in the original description, appears to be questionable. An adult male from Tatemales, Sinaloa, measured in the flesh by the collector: Total length, 892 mm; tail, 333; hind foot, 110. Skull: Two adult males from Los Masos, Jalisco, respectively: Greatest length, 93.2, 91.7; condylobasal length, 87, 85.9; zygomatic breadth, 65, 63.2; breadth of brain case, 39.7, 39.1; interorbital breadth, 16.8, 17; postorbital constriction, 31.1, 31.6; maxillary tooth row, crown length to back of carnassial, 27.2, 27.4; upper carnassial, crown length (outer side), 11.3, 11.7.

Remarks.—*F. w. glaucula* has been recorded in Jalisco, and northward on the warm, western side of the Sierra Madre to southern Sinaloa. It appears to be most closely allied to *oaxacensis*.

Specimens examined.—Two, from Los Masos, Jalisco.

Felis wiedii cooperi, subsp. nov.

Texas Margay

Type.—From Eagle Pass, Texas; no. 25, male adult, skin only, U. S. National Museum; collected by Col. S. Cooper, U. S. Army; entered in museum catalog February 13, 1852.

Distribution.—Known only from the type locality, but probably has an extended range in northeastern Mexico.

General characters.—Size medium; ground color "cinnamon-buff"; dorsal markings solid black, or with very small, indistinctly lighter centers. Similar in size to *oaxacensis* and *glaucula*, but differs conspicuously from both in longer pelage, and solid, or nearly solid black dorsal spots, instead of enclosed lighter areas.

Color.—Ground color of upper parts "cinnamon-buff," with a very thin, inconspicuous admixture of dusky hairs from top of head over nape and along median dorsal area to base

of tail, becoming clearer pinkish buff on flanks, outer sides of forearms and thighs; upper surface profusely spotted or striped with black as usual in the group, but spots of irregular size and shape 15 to 20 millimeters in diameter of solid, or nearly solid, black except on sides of thorax where very small buff centers are present; facial markings much as in other races, but black stripe interrupted between inner angle of eye and side of nostril; nape with three narrow black stripes; a rather broad black stripe continuous on median line from behind shoulders to base of tail; under parts "pale pinkish buff," with blackish brown spots across abdomen and on inner sides of limbs; a heavy black bar across throat, and three narrower, interrupted bars across under side of neck; feet pinkish buff, varied by small, indistinct brownish spots; outer sides of ears blackish, except whitish submarginal spots, the edges "pinkish buff"; tail marked with broad irregular brownish black bands, and narrower interspaces, the interspaces "pinkish buff" above, and "pale pinkish buff" below and at extreme tip.

Measurements.—Type: From dried skin and, therefore, not very trustworthy: Total length, 862 mm; tail vertebrae, 331; hind foot, 112. Length of pelage on rump, 22.5; length of longer hairs on upper surface of tail near middle, 28.

Remarks.—The skin on which *F. w. cooperi* is based was identified as *Felis pardalis* and entered as no. 25 in the mammal catalog of the National Museum, February 13, 1852. The catalog had been started only the day before, and it is therefore one of the earliest entries. The specimen has still attached a part of the original label bearing data corresponding with that in the catalog, but received little attention for many years. The back of the label bears the designation "*pardalis* group J.A.A." in the handwriting of J. A. Allen. The specimen was first assigned to the proper group by Ned Hollister, who wrote "near *glaucula*" on the label and published the record (Proc. Biol. Soc. Washington, vol. 27, p. 219, Oct. 31, 1914). No other example of the species from so far north has come to my attention, but there seems to be no reason for questioning the validity of the record and it indicates a range paralleling in northeastern Mexico those of northern representatives of various groups mainly tropical in distribution. This isolated specimen record tends to emphasize the comparative rarity of the species. The new race is named for the collector.

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SUMMARY OF THE LARGE WOLVES OF CANADA, WITH DESCRIPTION OF THREE NEW ARCTIC RACES

By Rudolph Martin Anderson

For more than one hundred years the systematic status of Nearctic wolves has puzzled zoologists, and since 1912 most writers have conventionally referred the wolves occurring over an area of one hundred degrees of longitude between Greenland and Bering Strait to *Canis tundrarum* Miller, type locality Point Barrow, Alaska. The writer at various times noted certain local discrepancies in the current assumptions, but deferred publishing opinions pending a lengthy quest for authentic specimens from key localities. The work in Ottawa was also retarded by lack of specimens of typical *tundrarum*, the pivotal race, from Alaska, and only in 1942 through the kindness of Professor E. Raymond Hall, Museum of Vertebrate Zoology, Berkeley, was it possible to obtain the loan of six topotype skulls of both sexes and of different ages. These specimens have been of great value in separating other races found farther east. Measurements and other date given by Pocock (1935) and others have clearly demonstrated that there are no great structural differences between the Eurasiatic and North American wolves of the arctic and subarctic regions. They are now generally considered to be subspecies of the circumpolar *Canis lupus* Linnaeus. The material at hand gives evidence that some of the native races of Canadian wolves are as large or larger than east Siberian wolves and should refute a widely spread popular belief in a comparatively recent influx of gigantic "Siberian wolves."

In the course of this work new material has come to hand rendering it desirable to revive the old name *Canis lupus griseus* Sabine (1823) for the large timber wolf of central and northern Saskatchewan, and to recognize the white wolf, *Canis lupus albus* Sabine (1823) as a tenable form that needs renaming because the name *albus* is preoccupied by *Canis albus lupus* Kerr (1792), applied to a white wolf from Jenesei River, northern Siberia. Two other Canadian wolves are here described as new subspecies.

Canis lupus griseus Sabine

Saskatchewan Timber Wolf

Canis Lupus-Albus Sabine, Franklin's Journey to the Shores of the Polar Sea, no. V, Zoological Appendix, p. 654, 1823.

Canis occidentalis Richardson, Fauna Boreali-Americana, 1829 (part).

Type.—Taken at Cumberland House, latitude 54°N, longitude 101° 40′ W, on Saskatchewan River about 35 miles northwest of The Pas, Manitoba, and about 15 miles west of the present Manitoba-Saskatchewan Interprovincial Boundary, during the residence of Captain [later Sir John] Franklin's first expedition to that place in January, 1820. The skin was preserved and deposited by Captain Franklin in the British Museum.

Distribution.—Forested regions of northern Saskatchewan and Manitoba, south formerly to the edge of the prairie region about Carlton. Saskatchewan; east into central Manitoba and extreme northeastern Minnesota, and presumably west to east-central Alberta; north to Lake Athabaska, intergrading with *occidentalis* in the region of the 60th parallel, with *hudsonicus* along the northern boundary of Manitoba; presumably intergrading in former times with *nubilus* in southwestern Manitoba and northwestern Minnesota and at present with *lycaon* in extreme western Ontario.

General characters.—The description by Sabine (1823, p. 654), also quoted in part by Richardson (1829, p. 66), is adequate: "It is very dissimilar in colour to the usual state of the [European] wolf, and is of a much greater size. . . . The teeth are remarkably strong and large; the ears sharp and erect, thickly clothed with dark-brown hair, tipped with gray; above and below on the neck the hair is thick and bushy; the whole of the body is covered with a mixture of long gray and black hairs, having some few white ones intermixed on the back; the sides and belly are dark gray; the tail is bushy, gray tipped with brown; the legs are strong, covered with dark-brown hair; claws strong, short, and arched."

Richardson (*op. cit.*, pp. 66–67) adds to this: "A specimen procured at Carlton House on the same river [the branch now known as the South Saskatchewan River], and now in the Museum of the Zoological Society (no. 33, Catalogue of the Museum) has the face, cheeks, throat, belly, hips and tail, white, except a small part of the latter, adjoining the rump,

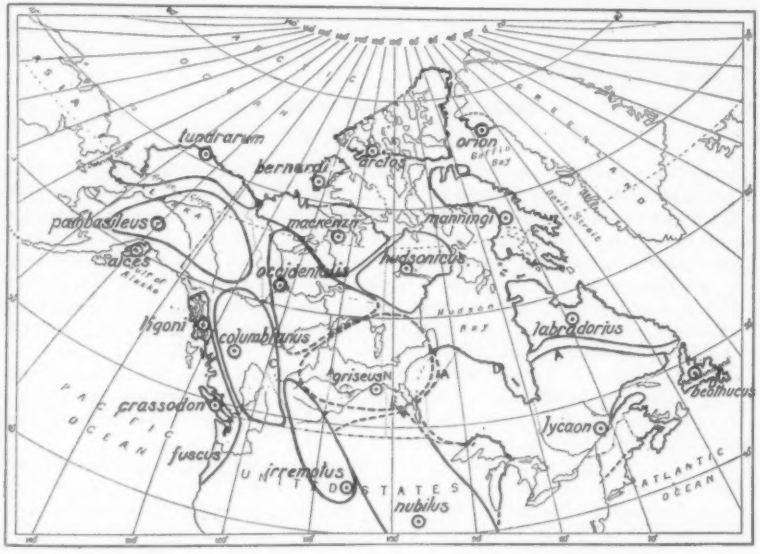

FIG. 1. Canadian races of *Canis lupus* (large timber and tundra wolves)

where it is blackish. On the back and sides there is an intermixture of long black and white hairs, which with the grayish wool that partially appears, gives a general grayish hue to these parts, deepening along the dorsal line into black. The hair on the back part of the cheeks is very bushy. In other individuals which I have seen, the mixture of dark-gray with black and brown forms distinct patches on an almost white ground. There is generally a darker line along the spine."

The above description applies almost exactly to an adult male (no. 17098) and an adult female (no. 17011) in the National Museum of Canada collection, and in fact would apply reasonably well as to colour to selected specimens of most of the northern races of wolves. The prolonged lumping of various forms under one heading has evidently been due to lack of sufficient skulls of adults for adequate comparisons.

Skull.—In general, averages larger in both sexes than in typical *occidentalis*; forehead straighter, with less concavity; occipital condyles generally narrower; bullae averaging larger and more rounded; coronoid process somewhat higher than in *occidentalis* and much

higher than in *columbianus*, with which *griseus* possibly intergraded in western Alberta in presettlement days; incisive foramina uniformly longer, more narrow and more curved than in *occidentalis*.

Measurements.—For the type specimen from Cumberland House, Sabine (1823) gives "dimensions as follows: length to the setting of the tail, four feet [1565 mm]; tail fourteen inches [356]; height to the top of the shoulders, two feet [610]." This would give a "total length" of 1821 mm. For the Carlton House specimen Richardson (1829) gives: "Length of head and body, 4 ft. 4 in. [1320 mm]; tail vertebrae 1 ft. 3½ in [394]; height of back, 2 ft. 2 in. [660]." The "total length" would be 1714 mm. No. 17098, N.M.C., ♂ ad., taken in Prince Albert National Park, Sask., Sec. 34–54, West of 3rd P. m., March 21, 1940, measured in the flesh: Total length, 1956 mm; tail 458; height, 864; weight, 93 pounds. No. 17011, N.M.C., ♀ ad., P. A. Nat. Park, west of Lavalle Lake, Feb. 16, 1940: Total length 1702, mm; tail, 483; hind foot, 289. For measurements of skull, see table.

Specimens examined.—Total number, 8, as follows: *Saskatchewan:* Prince Albert National Park, 3 ♂♂, 3 ♀♀. *Manitoba:* Riding Mountain National Park, 1, (taken in January 1943). *Minnesota:* St. Louis County, near Aurora, 1 (no. 30445 ♂, Mus. Nat. Hist., Univ. Iowa, Iowa City; taken in winter, 1938).

Canis lupus mackenzii, subsp. nov.

Mackenzie Tundra Wolf

Type.—Adult male, skin and skull; no. 2792, National Museum of Canada; from Imnanuit, west of Kater Point, Bathurst Inlet, District of Mackenzie, Northwest Territories, lat. 67° 44′ 20″ N, long. 109° 04′ 03″ W; collected May 14, 1916 (fresh specimen shot near camp by Eskimo) by R. M. Anderson, original no. 658.

Distribution.—Arctic coast and tundra region of Mackenzie District from east side of Mackenzie River delta, east to southern Victoria Island and Queen Maud Sea, south to northern and eastern sides of Great Bear Lake, upper Coppermine and upper portion of Back rivers, intergrading with *occidentalis* in southern portion of its range and presumably with *hudsonicus* to the eastward.

General characters.—Color variable, adults more frequently white, but adult specimens are often buffy with dorsal band of black-tipped hairs; some specimens are almost black. Considerably smaller than *occidentalis*, slightly smaller than *hudsonicus*, *tundrarum* and *bernardi*, and considerably larger than *manningi*.

Color.—The type specimen is entirely yellowish white with exception of brownish black spot on dorsal side of tail; claws pale horn color. A mounted female, N.M.C. no. 2551, shot near Bloody Fall, Coppermine River, Feb. 10, 1915, is even purer white, and type of *Canis lupus albus* Sabine (1823), taken at Fort Enterprise, about 230 miles farther south, is described as a white wolf. An adult male, N.M.C. no. 2791, taken at Port Epworth, Coronation Gulf, July 20, 1915, is yellowish white, with top of head tawny brown, mixed with black-tipped hairs; neck sparsely black-tipped, and dorsal region with most of hairs black-tipped; legs buffy brown anteriorly, white posteriorly. An adult female, N.M.C. no. 4868, taken on Kogaryuak River, Coronation Gulf, June 10, 1917, by Jos. F. Bernard, is mostly slaty gray, with hairs on back having paler brownish tips; legs and under parts mostly plumbeous or dusky.

Skull.—Much larger than in *manningi* of Baffin Island, smaller than in *hudsonicus* from west of Hudson Bay, and *tundrarum* from northern Alaska, with teeth about the same size as in the last two forms but larger than in *manningi*. Compared with *bernardi* from Banks Island, the teeth of *mackenzii* are much smaller, particularly the upper and lower carnassials. Ramus of mandible short and heavy, with lower edge of ramus much more convex than in *tundrarum*; coronoid processes lower than in *tundrarum* and with tips slightly recurved posteriorly.

Measurements.—Approximated from tanned skin of type male: Total length, 1676 mm.; tail vertebrae, 361; hind foot, 247. (Careful measurements of tanned skins of wolves in the N.M.C. show surprisingly little variation from measurements of the same animal taken in

the flesh.) Specimens of this race measured in the flesh by the writer are as follows: No. 2789, Rae River, west of Coronation Gulf: Total length, 1570 mm.; tail vertebrae, 385; hind foot, 281; weight, 78 pounds. No. 2551, ♀ adult and one other ♀ taken the same month on lower Coppermine River measured, respectively: Total length, 1565, 1460; tail vertebrae, 425, 470; hind foot, 285, 295.

Remarks.—Although the type specimen of *Canis lupus albus* Sabine (1823) could not be brought out from Fort Enterprise, a description of the specimen was published, giving locality, date and measurements, and illustrated by a fine plate entitled "The White Wolf and a View of the Dogrib Rock," subtitled "The Landscape by Lieut. (later Admiral Sir George) Back, R.N." and "The Wolf by Lieut. (Robert) Hood, R.N." The association of four distinguished explorers with this specimen—Captain (later Sir John) Franklin, R.N., Dr. (later Sir John) Richardson, the father of Canadian arctic and subarctic zoology, Admiral Back, who brought back much natural history from his later Arctic expedition, and Lieut. Hood, a promising young naturalist who lost his life on the famous overland trip from the mouth of Hood River, gives this wolf a decided historic interest, and it is unfortunate that the name given by Sabine is preoccupied by *Canis albus lupus* Kerr (1792). The names of Franklin, Richardson, Back, and Hood have already been applied to various items of geographical and zoological interest, and because the distribution of this race of wolf is, as far as known, entirely within the Mackenzie district, the subspecific name *mackenzii* is proposed.

Specimens examined.—Total number, 8, as follows: Mackenzie District: Back River, near head, 1; Coppermine River (Bloody Fall and mouth of Tepee Creek), 2; Kater Point, Bathurst inlet, 1; Kogaryuak River, Coronation Gulf, 1; Port Epworth, Coronation Gulf, 2; Rae River, west of Coronation Gulf, 1. (Four specimens collected by R. M. Anderson for the American Museum of Natural History in 1910–11, from Langton Bay, Caribou Pt., Great Bear Lake, Dease River, and Kendall River (orig. nos. 544, 547, 536, and 477) are referable to this race.)

Canis lupus bernardi, subsp. nov.

Banks Island Tundra Wolf

Type.—Adult male; no. 2796, National Museum of Canada; from Cape Kellett, southwestern part of Banks Island, District of Franklin, Northwest Territories, lat. about 72° N, long. 125° W; collected February 27, 1916, by Peter Bernard.

Distribution.—Known only from Banks Island, but probably also occurs on northwestern Victoria Island.

General characters.—Color mostly whitish, with less buffy than shown by average specimens of *mackenzii* and *manningi*; all specimens examined showing a greater or lesser number of blackish-tipped hairs forming a more or less distinct median dorsal line. A rather large rangy wolf, with long narrow skull, slender rostrum and exceedingly large upper and lower carnassials.

Color.—In the type specimen the general color is white with no yellowish tinge, except on back of ears. Top of head from nose to nape with hairs dusky gray at base and with short white tips, giving the hair a clean grayish appearance; a darker gray streak under each eye; cheeks and side of nose dull whitish, more grayish under chin. Mane very long, with hairs whitish at base, distal to this a broad black band, sometimes with white tip, but many of the hairs have a second black band at tip, making a hair with four distinct bands; blackish-tipped dorsal area overlapping on shoulders and hips, narrower medially and fading out on shoulders and thighs; tail thickly intermixed on dorsal surface with black-tipped hairs; white below and with tip black and the usual black spot on top of tail; feet white; claws blackish. No. 3505, adult female (allotype), Dec. 15, 1915, is almost completely white; ears light buffy at base, duller at tips; a faint trace of black-tipped hairs along median dorsal line from nape to tail; tail white, with the usual black spot on top, but with no black at tip of tail; claws horn color. One additional male and one adult female and a subadult male and female are between the above extremes. One young wolf of the year,

TABLE 1—*Cranial measurements (in millimeters) of adults of* Canadian races of *Canis lupus*

SUBSPECIES	SPECIMENS	GREATEST LENGTH	CONDYLOBASAL LENGTH	ZYGOMATIC BREADTH	WIDTH ACROSS POSTORBITAL PROCESSES	LENGTH OF MANDIBLE	HEIGHT OF CORONOID PROCESS	MAXILLARY TOOTHROW	UPPER CARNASSIAL (PM^4) CROWN LENGTH	UPPER CARNASSIAL, CROWN WIDTH	FIRST UPPER MOLAR, ANTEROPOSTERIOR DIAMETER	FIRST UPPER MOLAR, TRANSVERSE DIAMETER	LOWER CARNASSIAL (M_1) CROWN LENGTH
arctos Pocock (1935), Ellesmere Id., Bear Penin., Eureka Sound	3 ♂♂	261.9	237.7	142.2	62.7	190.8	71.4	106.0	26.8	15.8	17.0	22.1	30.6
banksianus, subsp. nov., Banks Id., Cape Kellett	type	252.0	233.0	136.0	51.5	190.8	72.0	107.0	28.0	16.0	18.0	25.0	31.0
	3 ♂♂	245.3	232.0	129.3	51.8	189.4	70.3	106.0	27.4	16.6	17.6	24.2	29.7
	2 ♀♀	238.8	219.0	120.0	50.4	173.9	67.0	101.4	26.0	15.4	17.4	27.0	29.6
columbianus Goldman (1941) B.C., Alberta, Jasper Nat. Park	1 ♂	282.0	258.5	152.0	68.2	191.8	77.2	107.5	25.8	15.5	16.6	23.0	30.0
	1 ♀	273.5	251.0	144.0	62.0	201.0	75.8	115.0	27.0	15.9	18.0	23.0	30.2
fuscus Richardson (1839), B.C. Kimsquit,		279.0	245.0	136.0	63.0	202.2	71.5	110.0	26.2	15.2	17.0	22.3	29.7
griseus Sabine (1823), Sask., Prince Albert Nat. Park	largest	283.0	261.0	150.0	64.5	208.0	82.0	114.5	26.0	16.0	18.0	23.0	30.0
	3 ♂♂	282.2	258.8	147.0	66.2	207.3	82.4	113.2	27.3	16.7	18.0	24.0	30.3
	3 ♀♀	267.5	258.8	135.8	58.3	195.7	77.8	104.3	26.4	15.3	17.8	23.0	28.6
hudsonicus Goldman (1941), N. W. T., Artillery Lake	2 ♂♂	269.3	247.0	142.8	63.5	201.0	75.0	113.0	26.5	15.1	18.0	22.3	29.2
	4 ♀♀	259.7	238.1	137.0	62.4	176.0	69.5	103.6	26.5	15.5	17.4	22.7	30.5
irremotus Goldman (1937), Alberta, Waterton Lakes Nat. Park	1 ♂	242.2	222.2	128.0	59.8	179.0	70.0	100.0	26.0	14.0	16.8	21.0	29.2
	1 ♀	—	—	122.3	60.0	184.0	70.5	100.5	24.0	15.0	15.5	21.5	27.5
labradorius Goldman (1937), Quebec, George River, near Ungava Bay	1 ♂	229.0	218.0	121.0	54.2	174.0	66.0	96.5	23.0	14.0	13.8	28.8	27.2
ligoni Goldman (1937), British Columbia, Port Simpson	1, unsexed	—	—	122.3	57.0	172.6	73.0	98.5	24.0	12.2	15.0	18.0	24.3

lycaon Schreber (1775), Quebec, Gatineau and Pontiac counties	2 ♂♂	234.0	221.5	—	55.4	167.0	69.0	95.5	22.7	13.4	16.4	20.0	25.8
	3 ♀♀	231.7	218.0	123.6	50.9	170.8	64.2	98.2	22.8	13.3	16.9	20.8	26.4
mackenzii, subsp. nov., Bathurst Inlet, Coronation Gulf	type	248.0	226.0	131.8	59.0	179.0	72.0	102.0	26.2	14.0	17.0	22.0	30.0
	3 ♂♂	251.0	228.8	132.8	58.3	184.5	70.0	102.6	26.7	14.3	17.3	22.3	29.0
	2 ♀♀	241.0	223 5	129.8	52.8	182.5	71.0	101.5	25.4	14.1	17.0	21.8	28.0
manningi, subsp. nov., Baffin Island	type	231.0	214.0	121.0	54.0	169.0	62.0	94.0	22.0	11.8	16.6	19.8	27.6
	2 ♂♂	253.5	227.5	137.5	66.0	183.0	71.3	103.4	24.3	13.9	16.0	20.3	27.9
	3 ♀♀	247.8	224.3	129.5	59.5	180.0	67.0	101.7	24.3	13.5	16.1	21.6	27.3
occidentalis Richardson (1929) all from Wood Buffalo Park, Alta.	largest	278.2	253.8	155.0	60.0	205.5	79.0	111.5	27.0	16.2	17.5	23.0	30.0
	5 ♂♂	269.0	248.2	148.5	61.9	200.8	77.5	109.8	26.7	15.0	17.5	23.0	29.5
	5 ♀♀	260.6	241.8	131.5	59.7	189.3	72.5	104.8	25.9	14.8	16.8	22.8	29.0
pambasileus Elliot (1905), Yukon Terr., Yukon River, near mouth of 60-mile River		281.0	262.0	157.5	77.5	215.0	88.0	117.2	28.0	17.0	19.8	24.0	31.2
tundrarum Miller (1912), Alaska	topotypes.	264.5	245.0	135.5	60.7	201.5	75.5	109.3	26.5	14.8	19.0	23.0	30.8
	2 ♂♂, 2 ♀♀	258.3	237.5	134.5	67.5	191.3	71.0	107.5	25.8	15.1	17.5	21.5	30.4

Two other races should be definitely included in the Canadian list, the Vancouver Island Wolf, *Canis lupus crassodon* Hall (1932), and the Northern Plains Wolf, *C. l. nubilus* Say (1823), with two others on the borderline, the extinct Newfoundland Wolf, *C. l. beothucus* Allen and Barbour (1937), and the West Greenland Wolf, *C. l. orion* Pocock (1935), but skulls of the above forms were not available and space does not allow quoting of previously published records.

taken September 9, 1914, at Cape Kellett, is remarkable in having no buffy coloring; whitish, with a fairly well-defined median dorsal area produced by sparse black-tipped hairs on dull whitish background; tail white with a few black-tipped hairs, black spot on top and black tip; in almost all respects a miniature of the adult male type.

Skull.—Distinguished by great comparative length, narrow zygomatic breadth, long, slender rostrum, and exceedingly large carnassials. Nasals narrower than in *tundrarum* and extending much farther behind posterior extensions of maxillaries and with shorter distance across postorbital processes. From its nearest neighbor on the north, *Canis lupus arctos* (of Melville Island, Sverdrup Islands, and Ellesmere Island) with which it might be expected to have the closest relationship, *bernardi* differs the most widely, with skull of only slightly less length, but much less massive, with narrower rostrum, lesser zygomatic breadth, lighter lower mandible, of less depth and more nearly straight. The tooth-row is about the same length as in *arctos*, but the molars and premolars are all longer, broader, and heavier; canines and incisors project forward at a noticeably greater angle. Coronoid process slender, sloping backward more than in *mackenzii* and *tundrarum*; ramus of mandible lower than in *mackenzii* and nearly straight as in *tundrarum*, but slightly less in depth and heavier horizontally; coronoid processes usually more truncated at tip than in these other races.

Measurements.—Tanned skins of type, and no. 3506, adult female, allotype, measure, respectively: Total length, 1870, 1562 mm; tail, 366, 362; hind foot, 261, 235. Field measurements of one male and one female which did not reach the museum are: Total length, 1625, 1422; tail, 432, 406; hind foot, 305, 254; height at shoulders, 813, 660; depth of chest, 406, 305; girth, 736, 660. For measurements of skull, see table.

Remarks.—With this well-marked subspecies is joined the subspecific name *bernardi* in recognition of two natives of Tignish, Prince Edward Island, Canada, well-known for many years in Alaska and Western Arctic—Peter Bernard, sailing master of the gas schooner *Mary Sachs* of the Canadian Arctic Expedition, 1913–18, who collected the type and four other specimens of *Canis lupus bernardi* and lost his life in the line of duty on a sledge trip in northern Banks Island in spring of 1917, and his nephew, Joseph F. Bernard, who made many voyages into the Arctic as master and owner of the gas schooner *Teddy Bear*, and collected many scientific specimens of mammals and birds, as well as ethnological material in the Northwest Territories, Alaska, and eastern Siberia, including one paratype of *Canis lupus mackenzii* referred to above.

Specimens examined.—Six skins and 8 skulls from the type locality.

Canis lupus manningi, subsp. nov.

Baffin Island Tundra Wolf

Type.—Female, young adult, skin and skull; no. 17236, National Museum of Canada; from Hantzsch River, east side of Foxe Basin, west side of Baffin Island, District of Franklin, Northwest Territories, lat. about 67° N, long. 24° W; collected December 7, 1938, by Tom H. Manning, original no. 70.

Distribution.—In all parts of Baffin Island from Hudson Strait to Pond Inlet; probably also on Bylot Island.

General characters.—Considerably smaller than any of the other Arctic wolves, but with somewhat larger skull and teeth than in *Canis lupus labradorius*, from south of Hudson Strait. Color somewhat variable, but adults are generally white, and juveniles and subadults have more or less buffy, often with black-tipped hairs along median dorsal line.

Color.—The type specimen has hair mostly pure white, with very faint tint of buffy on nose; ears pale buffy at tips; dorsal region with faint buffy tint; feet and tail white; tail with black spot on top but with no black at tip. Two subadult females (nos. 65 and 69, Manning collection) caught at the same place and supposed to belong to the same family group as the type specimen, have top of head faintly tinged with reddish buff, ears similar; a narrow black edging around lower lip and posterior portion of upper lip; back with longi-

tudinal wash of yellowish buff inclined to reddish, with a few dorsal hairs blackish at tip; black spot on top of tail and tip of tail blackish. No. 68, also a young female, has more grayish on head, with a narrow dorsal band intermixed with blackish-tipped hairs; sides buffy; under parts and tail pure white. The last specimen is almost identical with a specimen taken by the late Reynold J. O. Bray in January, 1937, at Piling, 69° north, on west coast of Baffin Island. A winter specimen, taken 1882–83 at Ashe Inlet, Hudson Strait, is pure white with black spot on top of tail.

Skull.—Much smaller and less massive than in *arctos* in all respects, with rostrum more slender and zygomata proportionately much smaller; bullae much smaller; carnassials much shorter and less massive; tooth-row shorter and all teeth smaller. Compared with *mackenzii*, *manningi* has much smaller skull and teeth, palate more narrow and with posterior end of nasals projecting less far behind maxillaries; bullae smaller, more elongated and subtriangular. Compared with *tundrarum*, from which it is still farther separated geographically, *manningi* shows even greater difference in size; coronoid process much lower than in *tundrarum* and sloping backward, rounded at tip.

Measurements.—Type: Total length, 1003 mm; tail vertebrae, 389; hind foot, 262. Adult male, no. 94, N.M.C., Ashe Inlet (from tanned skin) and one female adult from Foxe Basin (from tanned skin), respectively: Total length, 1588, 1524; tail, 387, 368; hind foot, 191, 191. For measurements of skull, see table.

Remarks.—This race is named in honor of Mr. Tom H. Manning, leader of three British Canadian Arctic Expeditions to Hudson Bay, Melville Peninsula, Southampton Island and Baffin Island, and who in addition to topographical explorations of much hitherto unknown land, made extensive and important collections and notes in several branches of natural history.

Specimens examined.—Total number, 13, all from Baffin Island as follows: Ashe Inlet, Hudson Strait, 1; Baffin Island, 1; Hantzsch River, Foxe Basin, 4; Pangnirtung, Cumberland Sound, 3; Piling, 69° north latitude, Foxe Basin, 2; Salmon River, Pond Inlet, about 72° 30′ north, 2.

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GENERAL NOTES

TWO RECORDS OF DALL'S PORPOISE (PHOCOENOIDES DALLI)

In their excellent paper on Dall's porpoise, Benson and Groody (Jour. Mamm., vol. 23 no. 1, pp. 41–51) have called attention to the scarcity of published records of porpoises of the genus *Phocoenoides*. In view of this I should like to place on record two specimens of *Phocoenoides dalli* now in the mammal collection of the Academy of Natural Sciences of Philadelphia.

The first specimen, A. N. S. P. no. 16012, was taken in Chatham Strait, between Chichagof and Admiralty Islands in Alaska by Mr. R. R. M. Carpenter during the summer of 1933. It consists of a skull, including the lower jaw. The sex was not recorded.

The second specimen, A. N. S. P. no. 20531, was captured in the Inside Passage, 50 miles north of Prince Rupert, B. C., by Mr. Wm. Jenks Wright on August 25, 1939. The skull and stylohyal elements of the hyoid bones were preserved. The sex was unnoted.

The following cranial measurements, in millimeters, refer respectively to no. 16012 from Chatham Strait and to no. 20531 from the Inside Passage north of Prince Rupert, B. C.: Total length, 324, 309; length of beak from base of notches (measured along midline), 141, 132; breadth of beak at base of notches, 99, 99; breadth of beak at its middle, 60, 60; breadth of intermaxillaries at same point, 33, 34; greatest breadth between outer margins of intermaxillaries proximally, 48, 50; greatest breadth of skull (squamosal), 193, 180; tip of beak to anterior margin of superior nasal opening, 183, 170; breadth between orbital processes of frontal, 162, 160; breadth between hinder margins of temporal fossae, 166, 151; total length of mandible, 258, —; depth between angle and coronoid process, 70, —.

These measurements agree very closely with the measurements of the type skull and with those of the two California skulls of Dall's porpoise.

The dental formulae are as follows:

$$\text{A. N. S. P. no. } 16012 — \frac{21\text{–}22}{28\text{–}27}$$

$$\text{A. N. S. P. no. } 20531 — \frac{24\text{–}23}{\text{x–x}}$$

In view of the variation (in the number of teeth) commonly found in Cetaceans among individuals of the same species, these Academy specimens closely approximate the type skull of *Phocoenoides dalli* in their dental formulae.—FREDERICK A. ULMER, JR., *Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.*

THE COLORADO PIKA

Just above Centennial in the southeastern corner of Wyoming lies the Snowy Range. For the past two summers I have lived in this majestic region studying *Ochotona princeps saxatilis*, the Colorado Pika. Through the cooperation of the United States Forest Service it has been possible to obtain specimens by trapping and shooting. A .22 caliber rifle using shorts was utilized in obtaining animals for dissecting purposes, but when used at a range of under fifty feet proved too destructive to the body. Several types of live traps were tried and each was successful in a certain way. The two most satisfactory types were those which were tripped by the animal upon entering. The first of these was a treadle trap made from an old orange crate.

This type also proved very popular with the marmots, who would go inside to eat the bait, and being much larger and stronger than the pika could force off the cover or eat through the wooden sides.

The second trap was built from a discarded syrup can and a rat trap. This was very effective when the animal entered straight from the front, though a pika crossing the pan from the side and releasing the spring was almost invariable caught in the midsection and strangled. Stones had to be used to keep the marmots from upsetting the traps.

The most successful method of obtaining live specimens was to dig them out of the rocks. This procedure is accomplished by finding a pika which had made its retreat into a rock pile that borders upon soil on either side and is thereby in reality a long trench filled with rocks.

By picking out the rocks in a straight line completely across this trench and clinking the face of the rock wall formed on the down hill side with small stones, it makes it impossible for the pika to escape up hill, the direction in which they tend to go. The worker then takes his place on the down hill side of the rock pile and begins his work of removing the rocks. As the size of the pile diminishes the pika will be heard bleating. With much labor the rocks can be moved and with care and agility a live pika is the prize.

TABLE 1.—*Body dimensions and parasite infestations of the pika—seven adult specimens*

NO.	WT. IN GRAMS	BODY LENGTH, INCHES	HIND FOOT LENGTH, INCHES	PARASITES				
				Tapeworm	Fleas	Caecal worms	Stomach worms	Sex
1	234.5	7.25	1.13	Yes	Yes	No	No	F
2	177	7.0	1.1	Yes	Yes	No	No	F
3	185	7.3	1.3	No	Yes	Yes	No	F
4	180	7.0	1.1	Yes	Yes	No	Yes	F
5	200	7.5	1.25	Yes	Yes	No	No	M
6	186	7.5	1.2	No	Yes	No	Yes	F
7	175	7.0	1.06	No	Yes	No	No	M

Of the seven specimens taken at random and listed in Table 1 it should be noted that five are females and only two are males. The usual number of embryos is between three and four in all specimens examined. In one case the newly born pika weighed 8.0 grams while four well developed embryos of another pregnant female weighed respectively 9.6, 10.23, 8.37, 8.78 grams (total, including chorions, 36.98 grams).

All specimens taken were examined for visible external and internal infestations of parasites. In every case fleas were found upon the pelage. Two cases upon dissection yielded stomach worms while one case contained caecal worms. Second to fleas the most common parasites were tapeworms. In several specimens the intestines were so infested with tapeworms that the passage of food was retarded. A careful weighing showed that as high as one fourth of the complete intestinal weight was composed of tapeworms.

The stomach of three dissected specimens yielded a quantity of small stones composed of pieces of jagged quartzite. One stomach contained thirty-six small stones ranging in weight from 0.06 grams to 0.001 grams. Their purpose has not been determined as they were found in both young and adult.

Except for the above foreign matter the entire food of the pika is vegetable. The choice food of the pika is the blossom of *Sieversia turbinata*. Pika colonies are most abundant where the pasture lots among the rock fields are most luxurious. The pika, besides eating daily from his hayfield, also stores up hay for the winter. He will scamper to the pasture and cut a bundle of plants almost as large as himself which are thus carried by mouth to the rock slides, often a hundred feet or so away. This freshly cut fodder is placed under the rocks where it is protected from weather and cannot be blown away. Here it slowly cures into hay.

The exact use of this hay, whether for food and bedding or food only, has not been determined. However, in the spring all that remains of it are a few dried stems. Year after year haystacks are built in the same location as layers of old stems mixed with droppings are often several inches deep. Where *Sieversia turbinata* was abundant, samples from the haystacks contained over 44 percent of this plant, yet in a barren windswept area on another section of the range where a colony was located, over 68 percent of the haystack was composed of Engelmann spruce twigs (*Picea Engelmannii*) with a sparse scattering of other plants.

In captivity the food eaten was similar to that of a rabbit and included lettuce, cabbage, raw potatoes, dandelion and grass; of the grains, oat meal, and a commercial cereal "Wheaties," proved to be the most popular. Bread and cinnamon rolls were also readily eaten. Dried fruits were completely ignored when put in the feed box and water never seemed to be used. The animals studied in captivity thrived well all summer, but were released in the early fall in their native habitat because of lack of adequate accommodations for them. —KEN MARTIN, *19594 Henry St., Melvindale, Michigan.*

CALIFORNIA LEAF-NOSED BAT TRAPPED BY DESERT SHRUB

Although bats are noted for their skill in avoiding objects during flight, they sometimes meet with disaster under unusual circumstances. Johnson (Jour. Mamm. vol. 14, p. 156, 1933) records the finding of bats caught on burdocks in the Eastern United States and because of the infrequency of such accidents the following observation seems worthy of record.

On February 11, 1942, while engaged in field work in the desert mountains bordering the Lower Colorado River valley in California, I discovered a California leaf-nosed bat (*Macrotus californicus*) securely fastened to a large desert shrub. The bat was dead and the manner in which it was fastened to the shrub showed that it had become attached while alive and had not been placed there by some other animal.

The shrub on which the bat was fastened was *Eucnide urens* Parry, a broad leafed plant belonging to the Loasa family (identification by Miss Bonnie Templeton, Los Angeles Museum) and closely resembles some of the mallows except that it is completely covered with minute stinging hairs and barbed pubescence. The spines are so tenacious that if objects such as clothing, hair, or skin come in contact with the plant, it is almost impossible to break away without great numbers of the leaves adhering to the object.

The spines of the plant held the bat securely by both wings and the ventral side of the body. The wings were spread in a manner indicating a struggle on the part of the bat to free itself. The tips of the large ears also showed numbers of the tiny spines penetrating their thin surface.

According to Miss Templeton, *Eucnide* is a nocturnal blooming plant, opening its pale yellow blossoms at dusk and closing them again at dawn. Numbers of dead and still living insects trapped among the spines of the plant brings one to a possible and quite logical explanation of the accident.

Macrotus californicus is a known feeder on moths and Orthopteran insects such as grasshoppers and large katydids. Therefore it is quite possible to picture this large-winged and rather slow-flying bat hovering over a shrub which attracts nocturnal insects of this type. A flick of the bat's wing against the spiny leaves would be all the spines required to ensnare one wing and cause the bat to lose control of its flight and swing its body full against the plant. Once this had happened it would be almost impossible for the bat to free completely all portions of its wings and body from the spines at the same time. Continued beating against the plant would soon wear down the bat's strength and death would ensue, thus leaving the bat in the position in which I found it.

This reconstruction of the accident is purely imaginative, but, with the evidence at hand, plausible.—KENNETH E. STAGER, *Los Angeles Museum, Los Angeles, California.*

UNILATERAL DISPLACEMENT OF THE INNOMINATE BONE IN SOREX

The abnormality here figured is, I believe, unique in the literature of anatomy of mammals other than man. It consists of the posterior displacement of the right sacro-iliac joint and the right innominate bone to the extent of a full vertebral segment. Extensive search of the literature, medical included, has not revealed another such example, except in man. The specimen showing the abnormality is an adult male *Sorex trowbridgii montereyensis*, no. 46722, Mus. Vert. Zool.

As a result of this displacement, the first sacral vertebra developed asymmetrically, the right side being similar in appearance to the last lumbar vertebra. The retention, by the first sacral vertebra, of the free, unfused characteristics of the lumbar vertebrae, and par-

ticularly the most posterior lumbar vertebra, is termed lumbarization. This abnormality, though rare, is known in man, and references to it are scattered through medical literature; see especially Blumensaat and Clasing (Ergibn. d. Chir. u. Orthop., vol. 25, pp. 1–59, 1932), who give the best discussion and include an excellent bibliography.

The condition of lumbarization may be either bilateral and symmetrical, or unilateral and unsymmetrical, and must not be confused with cases of supernumerary lumbar vertebrae, which are common, according to Weil and Van Dam (Presse med., vol. 42, pp. 1700–1702, 1934), in such domestic animals as the horse, pig, sheep, and goat.

Sacralization, which is the fusing of the last lumbar vertebra to the sacrum, is the reverse of lumbarization. In man the one type of abnormality occurs as often as the other, according to Leri and Luton (Bull. et mem. Soc. méd. d. hôp. de Paris, ser. 3, vol. 47, pp. 331–333, 1923), but lumbarization rarely comes to the attention of the physician, whereas sacralization often does, as it leads to disorders of the lower back. There could not be found any estimate of the frequency of these abnormalities in man.

Probably both abnormalities occur in all mammals. In fact, Welcker (Arch. f. anat. u. entwick., year 1881, pp. 161–192), in speaking of transitions from complete sacralization to complete lumbarization, states that he has observed the last lumbar and the first sacral vertebrae "in numerous inflections in man and in animals of very different groups." He fails to mention, however, which groups. Another report, of an abnormality bearing a close resemblance to the one here presented, was by Hoff (Arch. d'anat. d'histol. et d'embryol., vol. 2, pp. 433–446, 1923) in which he figures and describes at some length an asym-

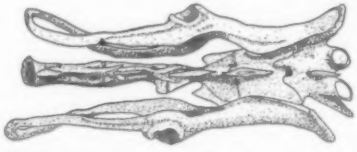

FIG. 1. Unilateral displacement of the innominate bone and asymmetry of the sacrum in *Sorex trowbridgii montereyensis*.

metrical sacrum of a lemur. He did not, however, mention the pelvis, and so it is not known whether one innominate was actually posterior to the other, or whether only the sacro-iliac joint on one side was posterior to the other, with the two innominates remaining at the same level in the body.

The condition of the shrew here figured is not, strictly speaking, unilateral lumbarization, although such cases in man are discussed (wrongly, I think) under this heading. The primary cause of the abnormality in this animal was the development of the right innominate one complete metamere posterior to its normal position, so that the first sacral vertebra on that side had no possibility of contact with the ilium and consequently developed more as a lumbar than as a sacral vertebra. True lumbarization should be considered to differ, in that the first sacral vertebra retains its lumbar characters in spite of the innominates occupying their normal positions.

In abnormal pelves of man, with unilateral displacement of one innominate, there would always seem to be an attempt at some type of compensation so that the pubic bones can be brought together into a symphysis. This tendency results in marked twisting of the spine and asymmetry of the pelvis, which has not occurred in the abnormal shrew figured here. Such compensation, however, would be more necessary in an animal such as man, which possesses a pubic symphysis, than in the shrew, which has none.

The slight asymmetry of the remaining sacral vertebrae of this shrew is typical for sacra with asymmetry of one vertebra. Otherwise the vertebral column of this animal is normal, both as to configuration and as to numbers of vertebrae.—CHARLES A. REED, *Museum of Vertebrate Zoology, University of California, Berkeley, California.*

REMARKS ON AMERICAN BISON IN LOUISIANA

The writer was interested in the recent note of Swanton (1941), giving the record of four bison killed in Louisiana in March, 1700, by the party of the French explorer and colonizer, Bienville, while on a journey from the Tensas villages on Lake St. Joseph to the villages of the Natchitoches close to the present town of the same name. Authentic records of large game in regions they formerly inhabited are valuable and rare. I had always taken it for granted, however, that bison were known to have been present in Louisiana in some numbers in earlier days, at least in the western part of the state.

My father, John Osbon Gunter, who lived all of his life in Natchitoches Parish, Louisiana, told me several years ago that buffalo were formerly present in the state and that buffalo wallows existed in the southwestern part of the state. The matter was never discussed further. When Dr. Swanton's note was published I decided to check on this information and wrote to Mr. E. A. McIlhenny, of Avery Island, Louisiana. I herewith quote, with his permission, part of his reply, dated September 9, 1941:

"Buffalo undoubtedly existed in that section of Louisiana lying west of the Teche and northern section of the Atchafalaya River. Fifty years ago, before the prairies of Iberia, Vermilion, Lafayette and prairie parishes west were settled, buffalo wallows were plentiful. Some of these wallows were on ridges in the prairies, and were at least 150 yards across. I judge the size, because I often stalked ducks and geese in these buffalo wallows, which were perfectly circular, and about sixteen to eighteen inches in depth, and often found the open water too wide to kill ducks across. Buffalo bones were frequently seen in the kitchen middens in the territory herein discussed. . I have, in digging these kitchen middens, frequently seen the upper part of skulls almost intact."

In another letter, dated December 13, 1941, he says: "Fifty or more years ago, there were numerous Indian mounds along the rivers of western and central Louisiana. It was not uncommon to find buffalo remains in the kitchen middens accompanying these mounds. I have not seen buffalo remains in the coastal section, but in the high prairies section, thirty to fifty miles back from the coast. Buffalo remains were almost always found in the mounds west of the Calcasieu River." He went on to say that most mounds have been torn up by souvenir hunters and that those remaining intact are in the swamp and marsh country.

Mr. McIlhenny says the circular ponds were present on the open prairies before the early settlers brought cattle to the country and were known in those days as buffalo wallows. He says that cattle congregate there now, to drink and fight insects and that probably the wallows have been enlarged by cattle.

Dr. Richard Joel Russell, of the School of Geology, Louisiana State University, has informed me that the buffalo wallows of Louisiana prairies are similar to the depressions described by Fisk, (Geology of Avoyelles and Rapides Parishes. La. Geol. Survey, Bull. 19, pp. 74–78, 1940.) under the name "pocks." They form under conditions of alluviation in flood plains. Channel positions change and successive scars become more or less filled by alluvium and organic debris as time goes on. The final remnants are the pocks. They may be as little as 10 feet across, or as wide as 1000, but are usually 100 feet or less. The horizon of the southwestern Louisiana prairies is late Pleistocene.

Dr. Fred B. Kniffen, of the Louisiana State University School of Geology, has written me he has what are thought to be bison bones from a number of archeological excavation sites in central Louisiana, but the bones have never been identified. Southwestern Louisiana has not yet been excavated.

As Prof. J. A. Allen pointed out years ago (1877), data on the early distribution of buffalo "exist in the form of incidental memorada in the narratives of the early explorers, rather than in formal statement" and are usually unsatisfactorily vague.

References to a number of historical records of bison in Louisiana have been obtained from various sources, but most have not been examined. Margry (1880), whom Swanton quoted, and de Montigny (1753) speak of buffalo in Louisiana. According to the latter, Bayou Terre Aux Boeufs, of Plaquemines Parish, was named for the large numbers of buffalo that spent the winter there. Margry mentioned another body of water referred to as Rivi-

ère Aux Boeufs. Du Pratz (1758, p. 67, Tome I.) said buffalo could not penetrate the woods and liked the high grass of the prairies. He stated that in winter the hunters left lower Louisiana and the Mississippi, to get the animals. Apparently he had reference in part to the prairies of western Louisiana as hunting grounds.

The most recent reference is that of Bry (1847). At that time the Commercial Review, later De Bow's Review, was running a series of historical articles on the various parishes of Louisiana. Bry's account deals with the history of the Ouachita region. According to him, John Filhial in 1781–82 was appointed commandant by the Spanish government and ordered to establish a post on the Ouachita River. He settled near Camden, Arkansas. "After having remained there four or five years . . . he came down to Monroe, where he permanently settled and established the *Post* of Ouachita, to which he gave the name Fort Miro. That spot being in a very eligible situation on the banks of the river, it was known to the hunters as Prairie des Canot, it being their common rendezvous from which they dispersed in search of game, then extremely abundant, and returned to descend to New Orleans, where they found a ready market for their peltry, bear oil, tallow and even buffalo meat, which was known in the city by the name of Viande du Chasse. The last buffalo seen in the neighborhood of Fort Miro was killed in 1803. A herd of about one hundred and fifty remained near the Bayou Saline, in Arkansas, about one hundred and fifty miles above Monroe, where, being surrounded with settlements, they were destroyed in 1807 and 1808."

Allen (1877), who reviewed records published up to his time, says in this area buffalo seem to have been absent only from the lowlands of the lower Mississippi, ranging "the higher prairie lands of Northwestern Louisiana and Arkansas." The writer believes that a thorough search of early literature would yield more references on bison in Louisiana. From the information presented here I believe we are permitted to conclude that: (1) Although specific records of kills of American bison in Louisiana are uncommon, the mention of the animals by early writers leaves little doubt that they were a part of the fauna of the state, and there are some indications that they were numerous at times; (2) Louisiana buffalo wallows are of geological origin, but quite possibly were used as wallows by buffalo.

I am indebted to J. Nelson Gowanloch for pointing out several references to me.

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GORDON GUNTER, *Game, Fish and Oyster Commission, Rockport, Texas.*

BOBCAT SWIMS

On the morning of June 3, 1942, at about 8:45 a.m., I was driving along the ditch of the All American Canal between the Laguna and Imperial dams on the Colorado River, 21 miles north of Yuma. I noticed an animal, which I thought was a beaver, swimming in the middle of the canal where it is about 150 feet wide. Upon driving closer, the ears indicated that it might be a coyote, and when I parked on the bank of the ditch directly opposite the animal, I could tell it was a mature bobcat.

It was a very good swimmer and had evidently selected a landing place on the opposite side, as it swam at an angle so that the current did not carry it down stream. Upon reaching the shore it crawled out and did not shake like a dog. However, it was watching me

closely as I was sitting in the car with the motor shut off. It glanced at the opposite side of the canal as if undecided whether to return and then proceeded along the ditch bank in the water for a short distance in front of the car before it climbed up and ran across the roadway and down to the brushy, marshy river country. It had just left mountainous desert country on the opposite side of the canal. All indications were that this animal entered the water of his own accord.—GENO A. AMUNDSON, *Yuma, Arizona.*

A COYOTE'S SPEED AND ENDURANCE

On December 19, 1941, Weldon B. Robinson of the Denver Wildlife Research Laboratory, and Preston Q. Hale, Junior District Agent of the Utah District, U. S. Fish and Wildlife Service, accompanied by two predatory animal hunters, made a trip onto the old bed of Lake Bonneville in western Utah. While crossing a section of the lake bed during the morning they observed a coyote in the distance, but the animal, evidently having had experience with automobiles before on this smooth sparsely vegetated area, immediately disappeared from view by crouching in the low vegetation. Although Hale and Robinson toured the approximate area for some time, they were unable to discover the coyote's hiding place. Some three hours later, on the return trip, a coyote, possibly the same animal, was again seen in the same general locality. This time when the coyote disappeared from view Hale and Robinson were able to mark its exact location. They drove to within 75 yards of the spot before the coyote, realizing its detection, jumped and began to run.

In the ensuing chase the coyote demonstrated its remarkable endurance and speed. It was able to elude its pursuers for 47 minutes from the time it was first observed until it was killed. At the start of the chase the coyote ran in a straight line for several hundred yards and was clocked by the speedometer on the car at the top speed of 43 miles an hour. It was able to maintain this speed for a relatively short distance, however, and never again approached that rate. Unable to out-distance the automobile, the coyote gave its pursuers a lesson in maneuvering. On several occasions it appeared as though the animal would be run over, but each time it was able to muster an additional burst of speed and emerge to temporary safety by cutting directly in front of the car and heading in a different direction. The animal, from all indications a two-year old in very fine condition, tired rather slowly, but still seemed to have some remaining stamina when it was finally killed.

While there have been many instances of trappers and hunters running down coyotes with automobiles, to my knowledge neither the maximum speed nor the length of endurance of a coyote has been accurately recorded. R. SCOTT ZIMMERMAN, *U. S. Fish and Wildlife Service, Salt Lake City, Utah.*

WHITE-FOOTED MICE FEEDING UPON GRASSHOPPER EGGS

The white-footed mouse, *Peromyscus maniculatus osgoodi* Mearns, a common rodent occurring in western North Dakota, was recently reported by Mr. Wm. Bauer, a farmer from Sioux County, N.D., as seeking out and feeding upon grasshopper egg pods. Through the courtesy of Mr. Bauer, eleven specimens were trapped and sent to the author. Upon examination of the stomach contents, three specimens contained eggs of the Differential Grasshopper, *Melanoplus differentalis* Thomas, a species which oviposits in the roots of grass clumps or weeds. The identification of the eggs was ascertained by comparing those ingested with eggs from a typical Differential pod collected in the field. The ingested eggs also agreed in every detail with the description and illustration of the Differential egg embodied in the publication "Identification of the eggs of Mid-western Grasshoppers" Kan. State Exp. Sta. Tech. Bull. no. 48, 1939, 39 pages, by J. B. Tuck and Roger C. Smith. The fact that the mice were collected in April, long before adult gravid female grasshoppers would normally appear, coupled with the absence of grasshopper body fragments in the stomach precluded the possibility of the mice obtaining the eggs by ingesting gravid grasshoppers.

Although these mice are primarily vegetarians, they commonly feed upon insects; however, there is apparently no previously published record of their feeding upon grasshopper egg pods. The author acknowledges the assistance of Dr. H. H. T. Jackson, in Charge,

Biological Surveys and Mr. A. L. Nelson, in Charge, Wildlife Research Surveys and Mr. A. L. Nelson, Wildlife Research Laboratory, Patuxent Research Refuge, both of the Fish and Wildlife Service, for confirming the author's determination of *Peromyscus* and for data on their food habits.—HORACE S. TELFORD, *North Dakota Agriculatural College, Fargo, North Dakota.*

DOUBLE CAPTURES OF SMALL RODENTS IN CALIFORNIA

Recent sylvatic plague investigations by the Hooper Foundation for Medical Research included the study of small mammal populations in the Transition Zone of the central Sierra Nevada at Bass Lake (elevation: 4500 feet), Madera County, in 1939 and in the Upper Sonoran Zone of the inner Coast Range at Calaveras Reservoir (elevation: 1000 feet), Alameda County, California, in 1940–41. A single-catch live-trap, manufactured by Young's Animal Trap Co., was used; the capture of two individuals in one trap suggested that they had entered together or in fairly rapid sequence. Such "double captures" occurred quite frequently in the course of trapping:

BASS LAKE	TOTAL NO. CAUGHT	INVOLVED IN DOUBLE CAPTURES
Peromyscus boylii	183	24
P. maniculatus	86	31
Perognathus californicus	18	4
Microtus sp.	3	2
CALAVERAS RESERVOIR		
Perognathus californicus	89	26
Peromyscus truei	69	24
P. maniculatus	52	29
Neotoma fuscipes	30	4
N. lepida	20	4
Reithrodontomys megalotis	1	1

Thus 43 percent of the *Peromyscus maniculatus*, 35 percent of the *P. truei* and 28 percent of the *Perognathus californicus* were involved in double captures. Of the 88 double captures recorded, 41 included individuals of different species and 47 those of the same species. There was a random distribution in combinations of the sexes.

In these double captures there were 44 instances where one or both of the animals were dead when found. This mortality was probably due in part to exposure, but in 25 instances there was evidence of fighting; 8 of these included individuals of the same species and in 17 two species were taken together. The most striking example of this was seen when *Perognathus* was caught with *Peromyscus*. In the 27 instances of this combination, evidence of fighting was observed in 16, with a total of 20 deaths for *Perognathus* and 6 for *Peromyscus*. *Perognathus* is evidently at a disadvantage when in a trap with *Peromyscus*, possibly because it cannot make use of its jumping ability. In contrast, there was evidence of fighting in only one of the ten instances when two different species of *Peromyscus* were caught together.

The frequency with which these small rodents were taken in double captures by single-catch traps suggests that individuals often are in rather close association with one another, particularly when foraging or engaged in similar competitive activity.—F. C. EVANS AND R. HOLDENRIED, *Division of Zoology, College of Agriculture, Davis, and Hooper Foundation for Medical Research, University of California, San Francisco, California.*

UNUSUAL INJURY TO YOUNG HARBOR SEAL

During the course of fur seal studies on St. Paul Island, Alaska, a baby male harbor seal (*Phoca vitulina*) was brought into the village by Agent L. C. McMillin and native foreman John Hanson. They had found the seal pup on the boulders of Northeast Point on Decem-

ber 3, 1941. He was completely denuded of all hair with the exception of small areas of the regular spotted coat on his head, under his fore-flippers, between the hind flippers, and around the uro-genital opening. Only an extremely short stubble protruded above the skin on the rest of the body, giving it a rough sandpaper-like feel. An attempt was made to keep the young seal in captivity inasmuch as he appeared normal in all other respects. He would not feed satisfactorily, and on December 8 he was found dead in his cage. Lack of nourishment was almost certainly not the cause of death since he was very fat and had not declined in weight to any extent. When the skin was removed his body was found to be a mass of bruises. Evidently the young seal had been buffeted among the lava beach boulders by heavy waves during one of the prevalent storms until the hair was worn away and the flesh severely bruised.

The weight of the seal was 26 lbs., indicating that he was not more than a few weeks old, since baby harbor seals reared in captivity are known to weigh about 20 lbs. when born. The measurements of this seal were: total length over curve of back—700 mm; tail—80 mm; girth—565 mm; length hind flipper—160 mm; width hind flipper, spread—210 mm.

Storm-killed fur seal pups (*Callorhinus ursinus*) are numerous along St. Paul beaches, especially in the autumn, but none was ever found showing the effects of abrasion that existed on this harbor seal pup.—Ford Wilke, *U. S. Fish & Wildlife Service, Patuxent Research Refuge, Bowie, Maryland.*

A FURIOUS WOODCHUCK

While carrying on a study of cottontails (*Sylvilagus* spp.) under the supervision of the Pennsylvania Cooperative Wildlife Research Unit I observed a pugnacious woodchuck (*Marmota monax*) on the morning of June 12, 1942.

Knowing that the activities of woodchucks are important in providing denning sites for cottontails, I had placed several box traps near woodchuck dens. One of these traps contained a two-thirds grown woodchuck on this particular day. The usual procedure of releasing these animals was taken, but this woodchuck did not run out when the door was opened. In an effort to hasten the release of the animal, I picked up the trap and proceeded to shake the woodchuck, which slid out the open door and looked around for an instant. Upon sighting his liberator he charged, with open mouth. Fortunately I had held on to the box trap, which I immediately threw to the ground in front of the charging animal in an effort to divert its attack. The woodchuck was travelling at such speed that he was unable to dodge the obstacle. He hit the trap a glancing blow and dashed on about eight feet before stopping. As the animal turned and looked over his left shoulder he saw me and charged again. This time there was no obstacle to divert his attack. I had sufficient time, however, to jump to the side as the furious animal rushed by. The surprising speed of the animal was manifested in the fact that he was unable to stop until he had charged past me about 10 feet. Again the woodchuck surveyed the situation. This time, he paid no attention to me and slowly ambled into the brush.

Many woodchucks were caught previous to this incident and many since, but none of the others gave the slightest indication of attack.—Fred A. Glover, *Department of Zoology and Entomology, Pennsylvania State College, State College, Pennsylvania.*

PEROMYSCUS MANICULATUS BAIRDII AND SOREX PALUSTRIS HYDROBADISTES IN THE LOWER PENINSULA OF MICHIGAN

In a recent article Hooper (1942) has discussed the distribution of *Peromyscuz maniculatus* and has shown that *bairdii* is most common in the southern half of the Lower Peninsula. It is of interest to report that two specimens of this subspecies were trapped on August 8, 1942, on the shore of Cecil Bay, Lake Michigan, at Wilderness State Park, Emmet County. This record pushes the known range of *bairdii* one county north of that given by Hooper, bringing it within a few miles of the tip of the Lower Peninsula.

Also trapped on this date at Wilderness Park was one specimen of the water shrew, *Sorex palustris hydrobadistes*. It was taken on the banks of a small stream about 50 yards

from the place where *P. bairdii* was caught. At this point the stream is sluggish, and heavily shaded by a dense growth of coniferous trees. This subspecies has been reported in the Upper Peninsula of Michigan by Jackson (1926), but there is only one record for it in the Lower Peninsula. Creaser (1934) reported the capture of one specimen in a wooded gorge near Douglas Lake, Cheboygan County.

I am indebted to Dr. W. H. Burt of the Museum of Zoology, University of Michigan, for identifying these specimens. The water shrew and one of the mice have been deposited in the Museum of Zoology, University of Michigan, at Ann Arbor.

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Harold B. Hitchcock, *University of Western Ontario, London, Ontario, Canada.*

MYOTIS AUSTRORIPARIUS IN TENNESSEE

In the course of identification of various bats in the collection of the Cleveland Museum of Natural History, a specimen of *Myotis austroriparius* (Rhoads) was recently discovered. This specimen, a young adult male, was taken by Morton L. Church at Indian Cave, Grainger County, Tennessee, on Dec. 24, 1911. This apparently constitutes an addition to the list of mammals known from the state. The species is not listed by Kellogg in his "Annotated List of Tennessee Mammals" (Proc. U. S. Nat. Mus., vol. 86, no. 3061; Feb. 14, 1939). The specimen was mistaken by Mr. Church for an example of *Myotis grisescens*, a series of which he took at the same place and time.

Myotis austroriparius is known from Mitchell, Indiana, on the basis of four specimens, and from Florida, where the species is not uncommon locally. The Tennessee record provides concrete evidence of an intervening distribution long suspected.—B. P. Bole, Jr., *Cleveland Museum of Natural History, Cleveland, Ohio.*

EXTENSIONS OF RANGE FOR THREE BATS IN CALIFORNIA

New information on the ranges of three Californian bats is supplied by the following hitherto unpublished records:

Myotis lucifugus phasma Miller and Allen. Great Basin Little Brown Bat. An adult male (no. 2088, J. C. von Bloeker, Jr. coll.), taken August 26, 1927, by Granville P. Ashcraft, at Mammoth Lakes, 9,000 feet altitude, Mono County, California, marks the third definite station of occurrence for this race in California. Previous records are from Shepherd Canyon, Argus Mountains, Inyo County (Grinnell, 1933, Univ. Calif. Publ. Zool., vol. 40, p. 86), and Keeler, Inyo County (Benson, 1940, this journal, vol. 21, p. 354).

The specimen from Mammoth Lakes agrees with the original description in the pallid coloration of its pelage and in having pale brownish ears and membranes (instead of blackish as in *M. l. carissima*). I am indebted to Dr. Seth B. Benson, of the Museum of Vertebrate Zoology, Berkeley, California, for identification of the specimen here recorded.

Myotis ruddi Silliman and von Bloeker. Rudd Black Bat. On July 4, 1940, I shot an adult female (no. 7168, Los Angeles Museum) of this species at San Emigdio Camp, 6,000 feet altitude, at the head of Cuddy Valley, Mount Pinos, Kern County, California. This extends the known range of *M. ruddi* 125 miles to the southeast of the nearest previously recorded locality. Up to this time the species has been known only from San Benito and Monterey counties, California.

Eumops perotis californicus (Merriam). California Mastiff Bat. James Silliman captured an adult female (field no. 377, O. P. Silliman coll.) of this large free-tailed bat which flew into the Mitchell-Silliman warehouse at Camphora, 175 feet altitude, 2 miles northwest of Soledad, Monterey County, California. This is the first known record of the mastiff bat in Monterey County. It also constitutes the westernmost record for California and about parallels the previous northernmost station of occurrence, which is, Mendota, Fresno County (Grinnell, *supra cit.*, p. 95).—JACK C. VON BLOEKER, JR., *Allan Hancock Foundation, University of Southern California, Los Angeles, California.*

DIPODOMYS DESERTI IN UTAH

Eight specimens of *Dipodomys deserti* were taken in early May, 1941, while on a collecting trip for the University of Utah. They were all procured from Beaverdam Wash, Washington County, in extreme southwestern Utah. Six were taken five miles north, and two from eight miles north, of the Utah-Arizona border. This is, to the best of my knowledge, the first reported occurrence of this animal in the state of Utah.

Considerable trapping was carried out, both on the benchlands above and immediately adjacent to the wash, and in the bottom. In every instance, these animals were taken in loose, shifting sand at the base of shrubs, in the bottom of the wash. While other species of the genus *Dipodomys* were taken on the benchlands, no *deserti* were captured. The limiting factor as far as this form is concerned appears to be one of soil. While the soil of the benchlands is largely sandy, with a few small scattered stones, little or no loose, shifting sand was observed. This loose, shifting sand seems limited to the bottom of the wash. Other environmental factors, such as food and cover, seem adequate.

This restriction of habitat is interesting and curious when one considers the following facts. It is readily discernible that the bottom of the wash is periodically inundated. Floods occur during the spring run off and also sporadically in summer due to flash floods, which are characteristic of the region. In both localities where these animals were trapped the wash is flooded from bank to bank, while farther down stream towards the Arizona border, certain marginal areas escape inundation. Hence, during these periods of high water, which last sporadically from a few weeks in the spring to just a few hours or less in summer, the habitat is nearly or wholly depleted of these animals. Some probably escape to higher ground during these periods of adversity and reenter the bottom once the flood has subsided. Others doubtless enter it from the small marginal areas that escaped complete inundation. This drastic periodic reduction of the population, leaving only small breeding nuclei, probably accounts for their paucity of numbers.

Another factor is that Beaverdam Creek is a tributary of the Virgin River, which is in turn a tributary of the Colorado River. *Dipodomys deserti* has been reported from along the Virgin River in southern Nevada. Hence, in addition to the aforementioned small breeding nuclei, it is possible that some restocking of the animals in this depleted area takes place from this source. This pathway is doubtless the emigration route into the state. Could it be possible that *Dipodomys deserti* has not been encountered farther up the Virgin River, due to the barrier effect of the Virgin River narrows? These narrows are only a short distance above the mouth of the Beaverdam Wash and are so narrow in places that the stream covers the bottom from bank to bank.

This demonstrates an interesting example of the struggle this animal is encountering in trying to establish itself at the extreme limits of its range. STEPHEN D. DURRANT, *Department of Zoology, University of Utah, Salt Lake City, Utah.*

BACHMAN'S SHREW EAST OF ST. JOHNS RIVER, FLORIDA

Interesting from the standpoint of distribution is a record of *Sorex longirostris longirostris* taken east of the St. Johns River in Florida. A single specimen was taken under a prone palmetto trunk in the dense palmetto and bay thicket which forms the edge of a bayhead on the University of Florida Conservation Reserve, Welaka, Putnam County. It was collected April 8, 1942, and was identified by Hartley H. T. Jackson. Measurements

are: Total length, 83 mm; length of tail, 35; length of hind foot, 11. The skeleton is in the Department of Biology collection, University of Florida.

The two previous records of this shrew from Florida are both from a low hammock five miles east of Gainesville, Alachua County (H. B. Sherman, 1928, Jour. Mamm., vol. 9, no. 2, p. 148; and W. F. Blair, 1935, Jour. Mamm., vol. 16, no. 4, p. 274.). It is worthy of note that all three Florida specimens have been taken in low, at least seasonally wet, situations.—JOSEPH C. MOORE, *Buechel, Kentucky.*

REVIEWS

Allen, Glover M.* EXTINCT AND VANISHING MAMMALS OF THE WESTERN HEMISPHERE WITH THE MARINE SPECIES OF ALL THE OCEANS. Special Publication No. 11 of the American Committee for International Wildlife Protection. The Intelligence Printing Co., Lancaster, Pa. 1942. pp. xv—620, illus.

Considerable attention has been focused of late upon the vanishing wildlife of North America, and more particularly that of the United States. Current works treat the mammals, birds, reptiles, fishes, and lower forms collectively; still others are confined to monographs of particular species. Here for the first time is presented a concise treatment of the mammals alone, not only of North America but of the West Indies, Central and South America, and the oceans as well—the picture is presented in hemispheric perspective with the oceans as background.

That there is much to be said in favor of monographic treatment of particular species one cannot argue, and it is perhaps from such treatments that we are to obtain the details of each situation. The treatment of each known mammal, either extinct or on the verge of extinction, in such a manner would be an insurmountable task and impractical from several points of view.

It is the opinion of the reviewer that Dr. Allen has made a timely and worthwhile contribution to our knowledge concerning the present status of the mammals treated. The author has brought together the many scattered records concerning little-known families, genera, and species. He draws freely from the records of the Biological Survey, from the published records of museums and other organizations interested in mammalogy, and from the personal records of collectors, hunters, and trappers.

One serious criticism of the work is the space allotted to the discussion of forms of subspecific rank. Eighteen subspecies of beaver (*Castor canadensis*) are treated. Likewise over 90 distinct forms of bears are considered, many of which are of subspecific rank. There is every likelihood that some of the forms of grizzly treated as full species (the influence of the Merriam school) are in reality only subspecies. This interpretation would reduce the forms treated and thus affect a saving of "wasted motion." While the committee was perhaps responsible for assembling the mass of material and Dr. Allen was charged with the organizational details and the final presentation in printed form, the responsibility of both must be acknowledged.

On the other hand if such meticulous attention is paid to subspecies, what is the justification for omitting such forms as *Dipodomys elator*, a full species of which only four specimens are known? The same criticism applies also to several other North American forms—*Lemmiscus curtatus*, *Zapus luteus*, *Citellus brunneus*, and *Scalopus aereus*, to mention a few of them. If one insists on including subspecies, *Dipodomys nitratoides exilis* was at one time considered extinct. It is now known to maintain its precarious position in reduced numbers, but it is surely in greater danger of disappearing from the North American fauna than the many beavers. Yet it is not included! In the opinion of the reviewer, the book unduly emphasizes the mammals of the Caribbean and completely overlooks many of the continental species that should have been considered.

*Died February 14, 1942.

In treating the spotted bat (*Euderma maculatum*) the author lists eight known specimens from as many localities. He states (p. 30) that "this apparent rarity has led to the belief that the species is actually a waning one, and for this reason is here included." Is there not the possibility of another interpretation—that the species is more common than the record shows and that the range is at best imperfectly known? It is possible that it does not rightly deserve the distinction of "vanishing" species. It would be far more logical with the present facts at hand to label it what it obviously is, "rare."

The book is divided into three parts, each being an account of the mammals of the area treated: North America and the West Indies, South America, Oceanic Mammals. The mammals are treated in phylogenetic relationship under each section. Thus one is able to find the Carnivora treated in three places. That there is some duplication in this respect is entirely justified as the arrangement facilitates search for particular species. One would look for the sea otter, e.g., under the section on "Oceanic Mammals." The agouti and musk ox, on the other hand, are treated under "North America and the West Indies."

Each species is presented under an outline, including common name, current Latin name, original description and type locality, important synonyms and a reference (where available) to a published figure of the skull, entire animal, or other diagnostic characters (teeth, antlers, etc.). Life history notes, past and present distribution, date of extinction or present status are discussed for most species.

The section on oceanic mammals is particularly enlightening for here the author treats in sympathetic manner the plight of seals, sea-lions, walruses, and whales as a result of the serious depletion caused by the exploitation of commercial sealers and whalers.

Conservationists particularly, either those actively engaged in conservation or lay students, have here a treatment that is at once a report and a challenge. There is much information, too, for the general mammalogist.—Lewis A. Follansbee.

Warren, Edward Royal. The Mammals of Colorado, Their Habits and Distribution. University of Oklahoma Press. xvii + 330, 50 pls. $4.00. Second Edition.

Naturalists interested in the mammalian fauna of the southern Rocky Mountain region will find Warren's revised account of The Mammals of Colorado, published posthumously, helpful. In it are discussions of the more than one hundred seventy species and subspecies of mammals known to occur within the political boundaries of the State.

Accounts are arranged as follows: Scientific name, common name, citation to the original description, statement of the type locality, average external measurements, description, distribution, and remarks, under which life history and ecological information are recorded.

In general, the author deserves commendation for a task well done, but his nomenclatural treatment of several forms leaves much to be desired. For example, on page 11 *Neosorex* is given as a subgenus and, immediately following, the same term is used as the generic name of the water shrew. Among the bats, the generic name *Nycteris*, rather than the currently recognized *Lasiurus*, is applied to the red and hoary bats; *Corynorhinus megolotis*, rather than *C. townsendii*, is used for the lump-nosed bat. Among the rodents, numerous instances of digression from currently recognized scientific names occur. Since the author does not give any reason for his choice of name, in instances where recent works by able systematists indicate that a name other than that used by Warren is desirable, the reader may find it difficult to place much reliance in the author as a systematist.

Expansion of the section on Life Zones, the inclusion of distributional maps, and a complete record of the specimens recorded or examined from Colorado for each kind discussed would have enhanced the usefulness of the book.

The book is well printed, neatly bound and attractive, indexed, and a distinct advance over the first edition.—W. B. Davis.

Gabrielson, Ira N. Wildlife Refuges. pp. xiii + 257, 17 figs, 32 pls. The Macmillan Co., New York. $4.00.

With the tendency for increased industrialization and utilization of all commercially valuable natural resources, many wildlife species have suffered at the hand of man. Several

of them have been depleted over much of their former range and some few are on the verge of extinction. *Wildlife Refuges* portrays the efforts that have been made by Federal and State governments, and also by several private enterprises, to stem this tide of depletion and to maintain and manage several hundred million acres of land for the benefit of both wildlife and man.

The book is divided into 17 chapters, treating, among others, such topics as Purposes, Values and Limitations of Refuges; Types of Refuges; and Management of Refuges. The various types of refuges are discussed at length, pointing out purposes, locations, problems, etc.

The author has visited most of the important refuges in North America. His accounts are authentic and based largely upon personal acquaintance with the problems.

In general, most of the book has little value other than in presenting the present status and past achievements of the wildlife refuge systems. The chapters on Purposes, Values and Limitations of Refuges, and Management of Refuges, however, fill a definite need and merit the perusal by all who have close association with refuges, their problems, and administration.—W. B. Davis.

RECENT LITERATURE

(Conducted by Gerrit S. Miller, Jr., Remington Kellogg, and Emma M. Charters)

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COMMENT AND NEWS

BOARD OF DIRECTORS MEETS

On April 30, 1943, eight Directors assembled in the U. S. National Museum, Washington, D. C. for the purpose of conducting the routine annual business of the Society. The annual reports of the Corresponding Secretary, Treasurer, and Trustees were reviewed and placed on file. The thirty-four names proposed for membership were accepted. Funds were alloted for the printing of the Journal and for operating expenses of the Corresponding Secretary, Treasurer, Executive Committee and Editorial Committee. President Howell reported that Viola S. Schantz had been appointed chairman of the Index Committee to replace A. L. Nelson, who has found it necessary to relinquish the work with the committee. That Committee is continuing its checking of the entries in the index files and hopes to have the complete manuscript ready for the printer in a few months. The Directors agreed that a nominal charge for the index should be made to members, the exact amount to be determined when final copy is prepared. W. K. Gregory was reappointed to the Board of Trustees for a three year term and Remington Kellogg was reelected as the Society's representative to the Division of Biology and Agriculture of the National Research Council for the period 1943–1946.

It was agreed that the present slate of officers would remain in office until an election can be held at a regular meeting of the Society. Because of the uncertainty of the situation, no action was taken on a meeting for 1944, but it was decided that at least a restricted meeting should be attempted if at all feasible.

In order to allow any member in the armed forces to suspend his activities with the Society and yet remain on the membership roles for the duration of his service, it was ruled that any member who is in one of the armed forces and requests that his name be removed from the active membership list shall not be dropped from the rolls until six months after his period of service is completed.

OBITUARY NOTICES

Oscar Perry Silliman

1876–1943

Oscar Perry Silliman died, in Salinas, California, on May 9, 1943. He was born October 1, 1876, 2 miles east of Watsonville, California, the son of Wyliys Augustus and Martha Ann (Gilman) Silliman, the grandson of Charles Oscar and Phoebe Anne (Trafton) Silliman and of Perry Gilman of Kennebec County, Maine, and great grandson of Charles Wyllys and Deborah (Cass) Silliman of Connecticut and Ohio. On June 20, 1897, he married Mathilda Neal (daughter of James M. and Esther Neal) who survives him as do several of their thirteen children and many grandchildren. O. P. Silliman attended grammar school and high school in Watsonville, California, graduating from the latter June 6, 1895. After six months in preparatory school he taught grammar school for four years, then farmed until 1907, when he entered the feed and grain business and later wholesale bean business in which he was engaged at the time of his death. In spare hours he built up large collections of birds and mammals from Monterey County, California, a large collection of bird's eggs and a library rich in rare natural history books. A member of the American Society of Mammalogists since 1924, Mr. Silliman has given substantial aid to at least three young mammalogists and his assistance in this and other ways will be greatly missed.—E. Raymond Hall.

William E. Saunders

1862–1943

Dr. William E. Saunders, charter member of the American Society of Mammalogists, died June 27, at his home in London, Ontario. During a life of 82 years, he became known as one of the best field naturalists in Canada. Besides carrying on an active business, he managed to do some field work in Mammalogy or Ornithology nearly every day, writing voluminous field notes and collecting specimens. He encouraged and developed a number of young naturalists, was a member of several scientific societies, and, to quote one of his many admirers, "he was one of the few 'old timers' who didn't become fossilized with age."—W. B. Davis.